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UNIVERSITY OF ALBERTA

AQUATIC INVERTEBRATE COMMUNITIES OF BEAVER DAMS IN A BROWN-WATER STREAM OF ALBERTA

BY

GILLIAN M. WILEY

(C)

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1991

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ABSTRACT

This study examines the invertebrate fauna of beaver dams in the Bigoray River, Alberta. The dams provided several types of habitat for aquatic invertebrates. The main habitat was wood, both submerged and partially submerged, but detritus was also important. Most of the wood in dams was fresh and undecayed. The larvae of Simuliidae and Hydropsychidae were common on the dams, and these larvae used the logs for attachment for filter-feeding. More than half of the 72 taxa collected from dams were detritivores, *i.e.* scrapers or collector-gatherers, which fed on fairly undecayed wood, and scavengers and shredders that probably lived in the allochthonous detritus trapped by the dam. A diverse group of predators lived on the dam but were likely opportunists, using the wood for concealment, resting and as a source of prey. Taxa preferring to live in lotic habitats (both erosional and depositional) and lentic situations and on macrophytes were all collected from beaver dams, and provide additional evidence for the presence of several different habitats on dams. *Pericoma kincaidi* (Diptera: Psychodidae) was univoltine in the Bigoray River and probably overwintered as a fourth instar larva. Mermithid nematodes parasitised Simuliidae larvae throughout the year; the free-living stages of this nematode were commonest in June. Beaver dams may be considered disturbed environments due to beaver activity, but the fauna found on dams appears to be able to recolonise disturbed areas within a short time.

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INTRODUCTION

Beavers and Their Effects in Streams

The development of ecological theory and use of experimentation in lotic habitats have largely been concerned with describing and understanding factors influencing benthic invertebrate communities (Barnes and Minshall 1983). These include variations in structure and function of benthic communities in streams of differing size, with differing disturbance regimes, and with differing sediment characteristics (Egglishaw 1964, Rabeni and Minshall 1977, Minshall and Minshall 1977, Reice 1980, Culp *et al.* 1983, Culp and Davies 1985). There are models that incorporate the effects of natural alterations of habitat upon community structure and function. And in this regard, beavers may represent an important, but to date often ignored, influence on community structure and function (McDowell and Naiman 1986).

Beavers, *Castor canadensis*, occur naturally in streams, ponds, and the margins of large lakes (Shelton 1966) throughout North America, except for the arctic tundra, peninsular Florida, and southwestern deserts (Jenkins and Busher 1979). Before the arrival of Europeans in North America, the beaver population was estimated at 60 – 400 million (Seton 1929). But by 1900, continued exploitation left *C. canadensis* almost extinct in the United States and Canada (Jenkins and Busher 1979). Today, with fewer predators, less demand for furs, laws regulating trapping, and an abundance of forage and habitat, the beaver population is increasing rapidly and is thought to be between 6 and 12 million individuals (Naiman *et al.* 1988).

As well as numerous physical features of lakes and streams (Slough and Sadleir 1977) and the absence of natural predators, food availability is an important determinant of habitat suitability for beavers (Lawrence 1954). Beavers eat leaves, twigs and bark of most species of woody plants growing near water, as well as many herbaceous plants, especially

aquatic macrophytes. However, they are usually selective, preferring species with low lignin to nitrogen ratio such as alder, birch, aspen and willow, which decompose relatively rapidly (≤ 20 yr.) (Naiman *et al.* 1986).

Beaver-induced changes to drainage networks are not localised or unusual. Where beavers remain largely free of trapping or management, their activities may influence a large proportion of streams in a drainage network (Johnston and Naiman 1987). Naiman and Melillo (1984) stated that 20–40% of the total length of 2nd to 5th order streams may be affected, although most dams occur on 1st through 4th order streams (Naiman *et al.* 1988). Where topography is suitable and food supply is adequate, dam frequency may be high (Naiman *et al.* 1988). For example, the drainage networks of boreal forests in Quebec have an average dam frequency of 10.6 dams/km^2 on ≤ 4th order streams, (Naiman *et al.* 1986).

Beavers influence biological events in streams through their wood cutting and dam building activities, although there are few instances where changes in any ecosystem component by beaver have been quantified (Naiman and Melillo 1984). Vannote *et al.* (1980), as part of the River Continuum Concept, characterised small streams as narrow, heavily shaded channels, receiving a large proportion of their energy inputs from the surrounding forest and having large standing stocks of coarse detritus. But where beaver are present, a redefinition of such streams is necessary; it would include numerous zones of open canopy, large accumulations of fine detritus, increased wetland area, increased biogeochemical interactions with riparian plants and soils, reduced inputs of allochthonous inputs per unit area, and concomitant adjustments in the functional attributes of the invertebrate community (Naiman *et al.* 1986).

Beaver activity results in many alterations to the natural stream channel (Hodkinson 1975, Naiman and Melillo 1984, McDowell and Naiman 1986, Naiman *et al.* 1986, Naiman *et al.* 1988, Pringle *et al.* 1988).

1. They modify channel geomorphology and hydrology. Beavers primarily alter the stream channel by impounding water, and this changes the annual stream discharge regime, decreases stream velocity, and gives channel gradient a stair-step profile.
2. Beavers increase retention of sediment and organic matter.
3. They create and maintain wetlands around impoundments.
4. Beavers modify nutrient cycling and decomposition dynamics. When impoundments are created and flood adjacent terrestrial terrain, nitrogen and phosphorus are leached, resulting in increased aquatic production over 1 or 2 years. An increase in nutrients also occurs when impoundments are drained and refilled, as nutrients previously trapped in sediments are released (Baxter 1984). However as beaver ponds age, the sediments tend to retain nutrients. Hodkinson (1975) studied the energy budget of an abandoned, spring-fed, beaver pond in Alberta and found that the allochthonous energy input tended to be highly refractive and rapidly became locked in the sediments. Thus, he concluded that his beaver pond was a highly accretive, heterotrophic system. This short term increase in productivity in the first few years after the appearance of an impoundment may continue for nutrients such as nitrogen. Although allochthonous nitrogen decreased in an impounded area of second order stream studied by Naiman and Melillo (1984), an increase in nitrogen fixation by sedimentary microbes in the beaver-modified area caused an accumulation of 1000 times more nitrogen than before alteration.
5. Beavers modify the riparian zone – as foraging is selective the vegetative community composition and amounts of allochthonous inputs to the aquatic environment are altered.

6. They influence the character of water and materials carried downstream.
7. Beavers modify habitat and this can ultimately influence community composition and diversity.

In beaver altered habitats, invertebrate community structure is uncharacteristic of assemblages typically found in low order streams. The invertebrate community represented in beaver-modified sites differs functionally from the community dominated by shredders and collectors which is the model proposed for low order streams by the River Continuum Concept (Vannote *et al.* 1980). However Minshall *et al.* (1985) state that the model should be considered as a general theoretical construct in which to compare stream systems. Beavers modify stream geomorphology. This causes deviations in many lotic properties associated with low order streams. And this, because these effects alter invertebrate community structure and function, results in a low order stream system more complex than would be suggested by the River Continuum Concept (McDowell and Naiman 1986).

The Effects of Beavers on Stream Invertebrates

Beavers affect the benthic invertebrate communities of streams through habitat modifications (Sprules 1940, Hodkinson 1975, Naiman *et al.* 1984, McDowell and Naiman 1986, Naiman *et al.* 1986, Naiman *et al.* 1988, Pringle *et al.* 1988). The density of macroinvertebrates in rivers unaffected by beavers tends to be greater in riffles than in pools (Minshall and Minshall 1977, Logan and Brooker 1983). This is supported by Sprule's (1940) findings on the effects of a beaver dam on a stream, although McDowell and Naiman (1986) found both density and biomass of invertebrates to be statistically higher in beaver-impounded pools than riffles during spring and summer (the densities and biomass in pools and riffles were statistically similar in autumn). Diversity at the genus level is often greater in unaltered sites, and this is due mainly to the replacement of running

water taxa with fewer pond taxa (Sprules 1940, Hodkinson 1975, Minshall and Minshall 1977, Logan and Brooker 1983, McDowell and Naiman 1986, Naiman *et al*. 1988).

Beaver activities also influence community function by increasing the absolute importance of collectors, predators and some shredders, while decreasing the relative importance of scrapers and other shredders in impounded sites (Sprules 1940, Hodkinson 1975, Minshall and Minshall 1977, Culp and Davies 1985, McDowell and Naiman 1986). Thus, running water communities dominated by Simuliidae (Diptera), net-spinning Hydropsychidae (Trichoptera), Tanytarsini (Diptera: Chironomidae), and scraping Ephemeroptera are replaced in impoundments by Anisoptera, Coleoptera, Hemiptera, Chironomidae (Diptera), Tubificidae (Oligochaeta) and filtering Pelecypoda (Mollusca).

Many studies have been concerned with the ecology of macroinvertebrates on submerged wood; other studies have described invertebrate communities and quantified energy budgets of beaver ponds in streams. However, no published study has addressed the question of what aquatic invertebrates, if any, are associated with the substrates (wood, detritus and mud) of the beaver dams per se. Beaver dams consist of sticks and logs meshed tightly together across a stream, and largely submerged in water. The habitat for animals on these sticks would appear to be similar to the habitat created on submerged and partially submerged wood. The invertebrate community associated with wood debris in streams may use the wood surface as a refuge, for resting, for net attachment or case-building (e.g. Trichoptera), as a substrate for pupation and emergence, for feeding (e.g. grazing of the aufwuchs layer), ingestion of wood tissue, and sub-surface boring. Faunal associations on wood range from (a) obligates – those largely dependent on wood at some life stage, or having a significant effect on wood degradation through feeding, or using wood for case building, to (b) opportunists – those that are more opportunistically associated with wood.

The state of decay of the wood also determines the invertebrates found on it (Dudley and Anderson 1982): New wood is colonised primarily as habitat. The wood is then

colonised by algae and microbes which provides food for collectors and grazers. The wood's structure is not much affected yet. Fungi then invade the wood, softening it and allowing ingestion and abrasion by scrapers, obligate wood gougers and generalised shredders. Their activity sculpts the surface of the wood, and provides more invertebrate habitat. Over years, fungal invasion allows oxygen to penetrate the wood, and borers can move in and speed the degradation process by feeding and by the transport of microbial inocules. Finally detritivores, such as oligochaetes, invade the wood, and then decay is similar to that found in soil or damp terrestrial habitats.

Thus, studies on submerged wood as a habitat for aquatic invertebrates would indicate that beaver dams may support an interesting and diverse assemblage of animals, and this assemblage may be unique in low order streams unaffected by beaver.

Since 1966, H. F. Clifford has studied limnological features of the North Fork of the Bigoray River (Clifford 1978). In the early 1980's, beavers built a continuous series of beaver dams on the stream at Clifford's previous study sites. The beavers eliminated the riffle area in that region of the river and dammed the stream to create pools of relatively deep water; hence the river at those sites now appeared more lentic than lotic (Clifford unpublished data). However, drift samples taken by Clifford (personal communication) indicate that a lotic fauna does exist in the stream. He theorised that a potential site for these riffle organisms would be on the face of the dams or in the dams themselves, since the water flowing over and through the dams could create a small semi-torrential environment. He sampled two dams and took benthic samples from the impounded areas upstream of the dams in 1986 and 1987. My analysis of Clifford's unpublished data indicates a fauna on the dams quite different from that found in the rest of the stream. Larvae of Simuliidae, *Dicranota sp.* (Diptera: Tipulidae), *Pericoma kincaidi* Quate (Diptera: Psychodidae), *Baetis sp.* (Ephemeroptera: Baetidae), Chironomidae (Diptera), Hydropsychidae (Trichoptera), Nemouridae (Plecoptera), Hydracarinidae (larvae, nymphs and adults) and

adult Dytiscidae (Coleoptera) were found on the faces of dams but were scarce or absent from the extensive impounded areas. Some invertebrates, such as simuliids, chironomids, *Baetis*, hydropsychids and Hydracarina, were found in very large numbers. Therefore Clifford's findings (since 1969) provide a good basis for comparison of conditions in the stream before and after dams were established on it. There are no reports of *Pericoma kincaidi* in Alberta, and although the life-cycles of some common British genera of Psychodidae have been determined, the ecology of *P. kincaidi* has largely been ignored. On this basis I decided to examine its life-cycle on the dams.

I attempt to answer several basic questions about aquatic invertebrates found in this brown-water stream of central Alberta. Do differences exist between invertebrate populations in beaver dams and those in beaver pools in terms of population diversity? How are the invertebrate communities in the dams structured in terms of habitat preferences and trophic relationships? How might disturbance affect the fauna of beaver dams? What are the life-cycles of some of the invertebrates found in dams?

DESCRIPTION OF STUDY AREA

General Description

The Bigoray River at the study site is a third order brown-water stream located in west-central Alberta (Figure 1 and Plate 2). Canadian boreal forest regions are often drained by many slow-moving streams, termed muskeg or brown-water streams, which vary in size from trickles to large rivers. All have one feature in common: the dark colour of the water due to humic or fluvic acid from the surrounding poorly drained, muskeg-type terrain.

The Bigoray River is part of the Athabasca River system and Arctic Ocean drainage and is located 130 km west of Edmonton, on the dry continental side of the Cordillera. The climate of the region is subarctic by the Koeppen classification and the area is underlain by Cretaceous and Cenzoic sedimentary rock. According to Waksman (1938), the muskeg (organic terrain) drained by the Bigoray River would be classified as close to lowland peatland, forming from decomposed sedge and reedlike plants and characterised by water of low acidity. The Bigoray River was divided into three longitudinal zones by Boerger (1978): a headwater zone extending for 20 – 25 km, a middle zone extending for about 50 km, and a lower zone around 5 km long and terminating when the Bigoray River empties into the Pembina River. The middle zone has an average gradient of 0.1% and current velocity is less than 1 $cm.sec^{-1}$, although velocities as high as 30 $cm.sec^{-1}$ are found in constricted areas, for example below beaver dams and during spates (Boerger 1978).

The stream passes through sedge fens and bogs, and the surrounding flora is typical of muskeg regions of the boreal forest, being dominated by black spruce *Picea mariana*, tamaracks *Larix laricina*, and a number of *Salix* species (willow). The stream is U-shaped in cross-section and its bottom consists of clay, silt and gravel. Aquatic macrophytes, mainly *Hippuris vulgaris*, *Potamogeton richardsonii*, and *Sparganium*

angustifolium, appear from June to late August, and in late summer large mats of filamentous algae *Microspora loefgrenii* have been reported. Fish present include white sucker *Catostomus commersoni*, and less commonly burbot *Lota lota*, arctic grayling *Thymallus arcticus* and northern pike *Esox lucius*, (Clifford 1969). Beaver dams are numerous in the middle zone.

Description of Beaver Dams

Dams #1 and #2 are located in the middle zone of the Bigoray River. Dam #1 is about 100m upstream of dam #2 (Plate 1). Dam #1 is the larger dam measuring approximately 25 m in length and 2 m – 3 m in width. It projected 0.25 m above the upstream water level and 1.5 m above the downstream level, but water levels in relation to the dam changed depending on precipitation in the area (Plate 2). On some sampling dates, both dams were under a meter of water; conversely, in dry weather, the dams were more exposed than normal (Plate 4). Dam #2 measured 20 m x 1.5 m and generally projected a few centimeters above the upstream water level and 0.5 m above the downstream water level (Plate 3).

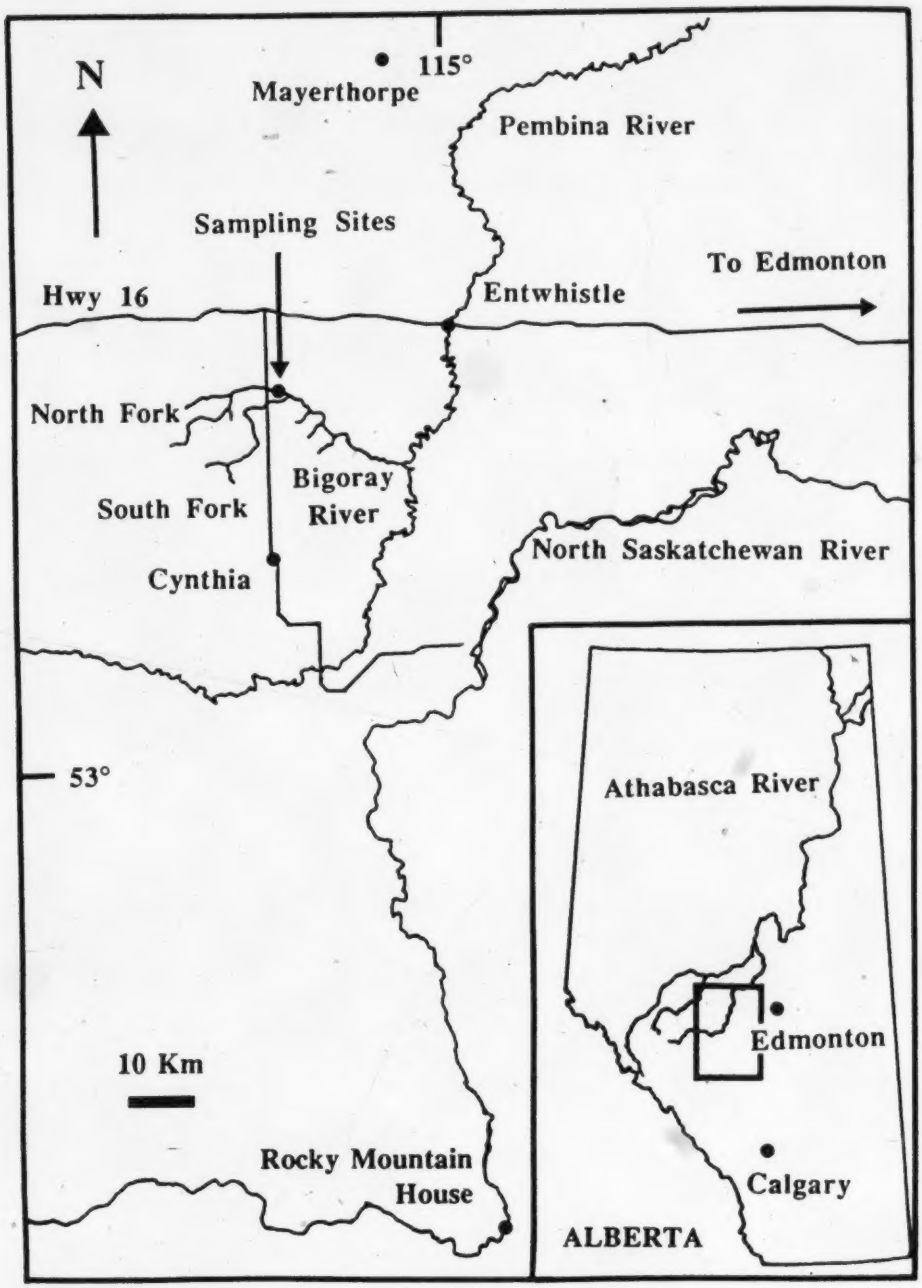
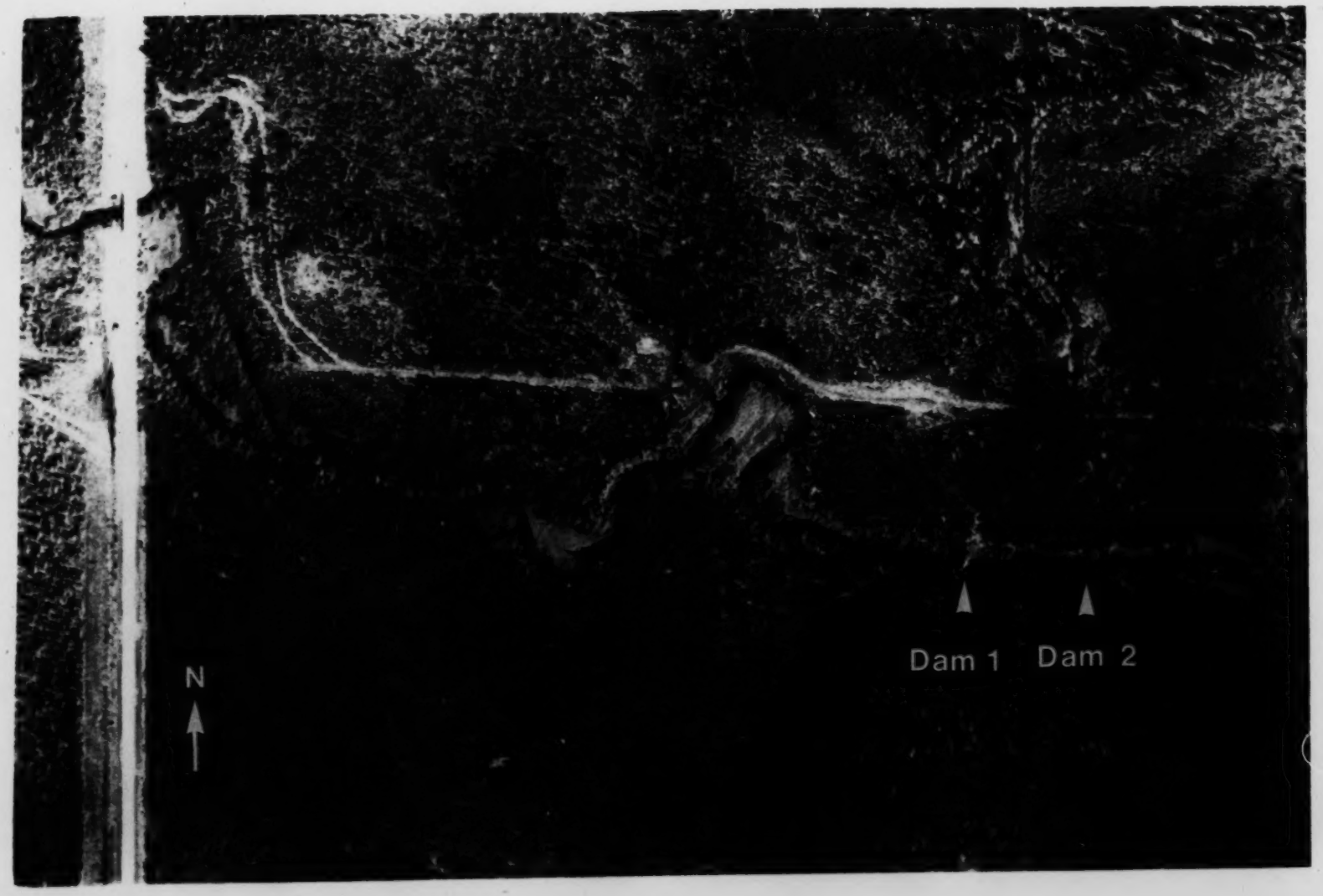


Figure 1. Location of the Bigoray River in Alberta.

Plate 1. Aerial view of the Bigoray River, 1988. Scale 1:3892.
The road on the left of the plate is Highway 753.


N
Dam 1
Dam 2

A.

B.

Plate 2. Dam #1 A. 8 Jun., water level in river is 19 cm.
B. 25 Aug., water level in river is 19 cm.

A.

B.

Plate 3. Dam #2 A. 1 Jun., water level in river is 20 cm.
B. 15 Jun., water level in river is 34 cm.
Emergence traps are shown in both plates.

A.

B.

Plate 4. A. Dam #1, flooding, 29 Jun., 1989.
B. Dam #2, snow-cover, 5 Apr., 1989.

METHODS

Physical Measurements

Water temperatures were monitored continuously by means of two Ryan-Peabody D-30 thermohydrographs. These were suspended just below the second dam in water about 1.5 m deep. Water temperature readings were also taken using a mercury pocket thermometer on each sampling date.

Conductivity readings were taken on each sampling trip using a Brinkmann Conductometer E587. Measurements were taken in the stream channel close to the bridge. A graph of conductivity plotted against temperature was prepared in the laboratory and used to standardise conductivities obtained in the field at different temperatures with those expected at 15 °C. (See Appendix 1 for the curve obtained in the laboratory.)

A stick was pushed firmly into the substrate upstream of dam #1 and water level measured from the top of this stake.

Kick Samples

Samples of benthic macroinvertebrates on the dams were taken at 7 to 21 day intervals between April and October, 1988 and between February and November, 1989 (sampling on dam #1 did not commence until April 1989 due to snow cover in February). I used a variation of the kick-sampling technique for sampling.

Collection of invertebrates proved to be challenging because the beaver dams are solidly constructed and difficult to sample quantitatively. I considered inserting sticks of a known area in the dams and removing them after a period sufficient to allow colonisation by aquatic invertebrates, but this did not work because the dams were actively being worked by beavers and such "inserts" were normally removed by the beaver before the proposed removal date.

Mackey *et al.* (1984) found that qualitative sampling of macroinvertebrates with a pond-net gave better results than with Surber samples or core samples for producing species lists. They also stated that the same method and operator should be used if comparison of samples was a requirement of the study. Taxon yield can be optimised by maximising the number of sites, and increasing the number of sampling occasions will minimise the chances of missing seasonal taxa.

To calculate diversity, it is important to collect as many taxa as possible for a given sampling effort. Where efficiency of collecting species is a major criterion, the pond-net is generally considered to perform at least as well as any other method (Morgan and Egglishaw 1965, Macan 1974, Mackey *et al.* 1984). Frost *et al.* observed that a series of smaller pond-net samples were consistently less similar than larger samples and that only a relatively small proportion of the available individuals were captured.

Mackey *et al.* (1984) examined the effects of reducing taxonomic level on taxon accumulation curves. They showed that, at the family level, one pond-net sample (generally a 5 minute kick-sample) was sufficient to collect over 90% of the families necessary for a representative list of taxa (they estimated that six samples provided such a taxon list). At the genus level, no more than two samples were required to obtain 90% of the genera collected in six samples. Therefore, although the authors suggested that six samples were necessary to compile a representative list of taxa, two samples would appear to be adequate for my identification purposes.

I used an adaptation of the kick-sampling method frequently used by workers on benthic stream communities. I selected areas of the dam where water flowed over or through the sticks, either on the top of the dam (during high water) or on the downstream breast of the dam. Holding a long-handled pond-net, of mesh size 153 µm, downstream of the sampling area and close to the substrate, I vigorously agitated the sampling site by kicking the substrate of the dam and pulling sticks and detritus out by hand. Debris and

animals thus dislodged were carried into the net by the water flowing over the dam. Where the water current was too weak to do this, detritus and sticks were pulled from the dam by hand and constituted a sample. The areas sampled covered roughly 75 x 75 cm per sample and each "kick" lasted 1 to 2 minutes. However, despite my efforts to standardise methods, the results are only semi-quantitative due to the spatial and temporal variability of the substrate I sampled.

Samples were transferred into plastic bags and brought to the laboratory where they were either held at a temperature of 2.5°C or divided into fractions and preserved in 70% ethanol. Whether sorted fresh or preserved, samples were sieved into two fractions, one retained by a sieve of mesh size 500 µm and the other by a mesh size of 125 µm. The larger fraction was sorted by eye by placing a small amount of sample at a time in a white sorting tray, flooding with water, and removing all animals to a vial of 70% ethanol. The smaller fraction was sorted in petri dishes under a light microscope at 12x magnification.

Identification

Preserved macroinvertebrates were sorted in the laboratory and identified to genus or to the lowest feasible taxonomic level, using the following keys: Clifford (unpublished taxonomic keys), Quate (1955 – Psychodidae), Currie (1986 – Simuliidae).

RESULTS

Physical Characteristics

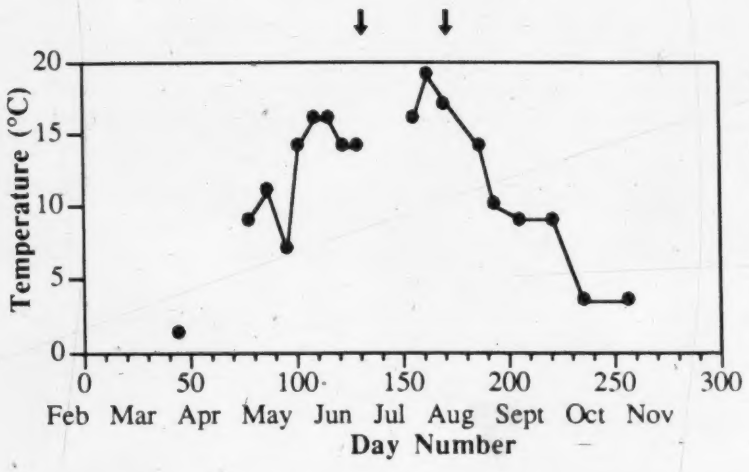
Temperature. Water temperature ranged from 0.5°C to 19°C during 1989. Water temperature reached a maximum in early August and also peaked at a slightly lower value (16°C) in mid-June (Figure 2A). Continuous temperature recordings showed that daily water temperature variations were between 0.0 and 2.5°C.

Ice-cover. Ice broke up between 5 and 25 April, 1989, and had reformed by 3 November; thus the river was ice-free for approximately seven months. Temperature and ice-cover data for the Bigoray agree with data on the seasonality of this stream from studies conducted between 1968 and 1977 (Clifford 1978).

Water level. The Bigoray River was flooded twice during the 1989 sampling season, on 29 June, and 9 August. On both occasions the water was too high to sample the dams, the sampling sites being under more than a meter of water. Apart from these two spates, the water level varied by a maximum of 50 cm between April and October (Figure 2B).

Conductivity. Conductivity reached a maximum of 331 micro-siemens per centimetre (μS/cm) immediately after ice break-up in April; conductivity also markedly increased in October. Minimum conductivity was 97 μS/cm on 29 June and corresponds to the high water at that time. Conductivity appeared to be inversely related to water depth (an indication of discharge) in the river; conductivity dropped sharply during each period of high water (26 May, 15 June, 29 June and 9 August) and increased as water levels fell (e.g. 1 August). However a regression of water depth against conductivity was inconclusive (Figure 3: $r^2 = 0.220$, $p < 0.1$, $n = 14$).

A.



B.

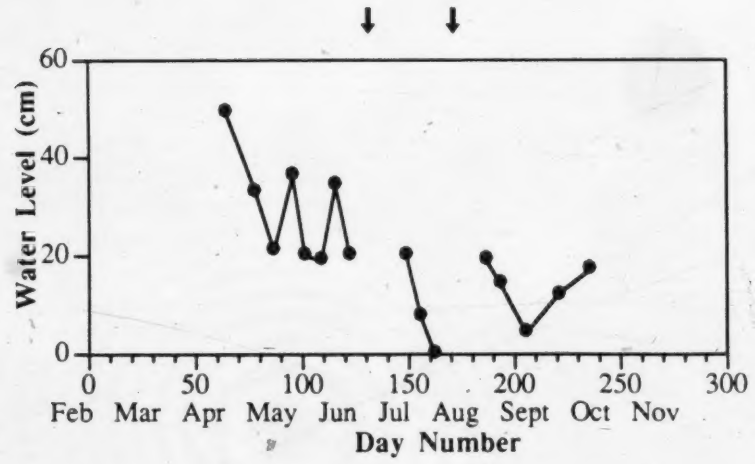


Figure 2. A. Water temperature in the Bigoray River, 1989.
B. Water depth in the Bigoray River, 1989.
(Arrows correspond to the dates of floods in the river)

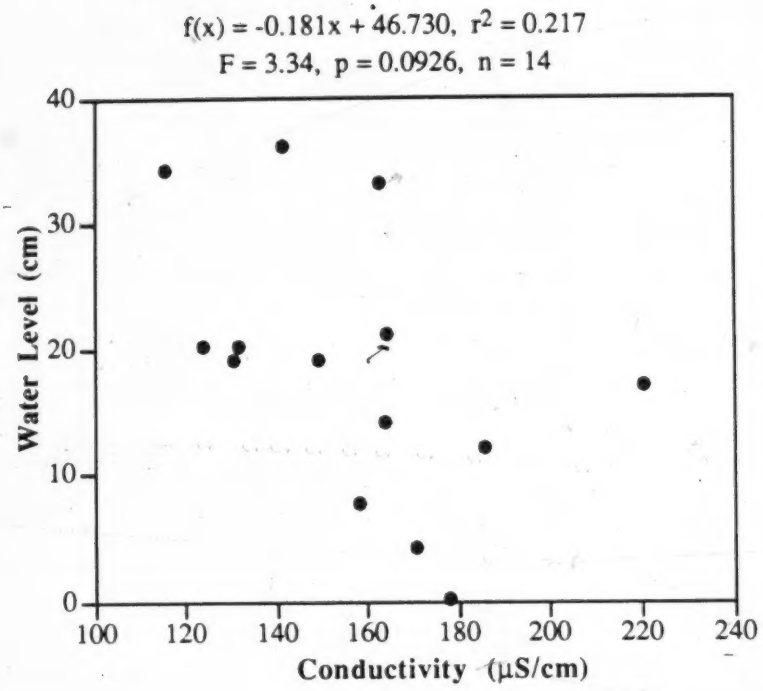


Figure 3. Conductivity plotted against water level in the Bigoray River, 1989.

Faunal Diversity

The diversity of benthic invertebrate taxa found on the dams was calculated using the Shannon-Wiener index (Pielou 1977, Krebs 1985):

$$H' = -\sum_{i=1}^{s} (p_i)(\log_2 p_i)$$

where H' = index of taxon diversity

S = number of taxa

p_i = proportion of total sample belonging to the ith taxon

Because this diversity index is strictly defined only for censused populations, and I estimated diversity from a sample of invertebrates in my study, the estimate is subject to sampling error.

Faunal diversity on dams and in the connecting river channel in the Bigoray River during 1986 showed some interesting trends (Figure 4). Analysis of dam samples indicated that diversity was low in the spring and autumn (0.17 in early May and 0.15 in November respectively) and had a peak of 0.27 in late May and a lesser peak in late August. Faunal diversities in the river channel connecting the dams were generally much lower than those of the dam. In the river channel, maximum diversity was reached in early May and November (diversities were 0.15 and 0.18 respectively); diversity was lower than 0.13 between those dates.

Since number of organisms per pond-net sample varied widely during 1989, ranging from averages of 415 to 40897 on dam #1 and 55 to 27061 on dam #2, I tested whether these differences affected calculations of macroinvertebrate diversities. The average number of invertebrates for each sampling date was regressed against diversity for dams #1 and #2. No significant relationship was found between sample size and diversity for dam #1 or dam #2 during 1989 (Figure 5A (dam #1): $r^2 = 0.188$, $p < 0.1$, $n = 17$. Figure 5B(dam #2): $r^2 = 0.016$, $p < 0.6$, $n = 19$).

It is evident from the inconclusive results of the regression analysis performed on the

numbers of invertebrates collected from the two dams that sample sizes on the dams tended to vary widely (Figure 6A: $r^2 = 0.213$, $p < 0.1$, $n = 17$). Despite this, faunal diversities on the dams were found to be related (Figure 6B: $r^2 = 0.682$, $p < 0.001$, $n = 17$).

Chironomidae and Simuliidae larvae, when each is considered as an individual taxon, formed a large and variable percentage of the invertebrates collected from both dams during 1989, and these high numbers tended to obscure the diversities obtained for the many less abundant taxa on the dams. Therefore, I excluded Chironomidae and Simuliidae and recalculated diversities for each sampling date, hereafter referred to as diversity (-C&S) (Figure 7). Diversities for both dams tended to be lower following the exclusion of Chironomidae and Simuliidae although this diversity followed roughly the same pattern as total seasonal diversity over the season. For dam #1, total diversity (including C&S) was high from May to late June, declined from July into September, and then sharply increased in October and November. This contrasted to the pattern when Chironomidae and Simuliidae were excluded from diversity calculations. Diversity (-C&S) peaked sharply in May and again in early June, dropped steeply in June, and remained low until October (Figure 8A). The pattern was similar for dam #2. Total diversity for dam #2 fell in May, increased over the summer, decreased again in late August, and increased in October; whereas diversity (-C&S) peaked in May, fell during the summer, and rose slightly in November (Figure 8B).

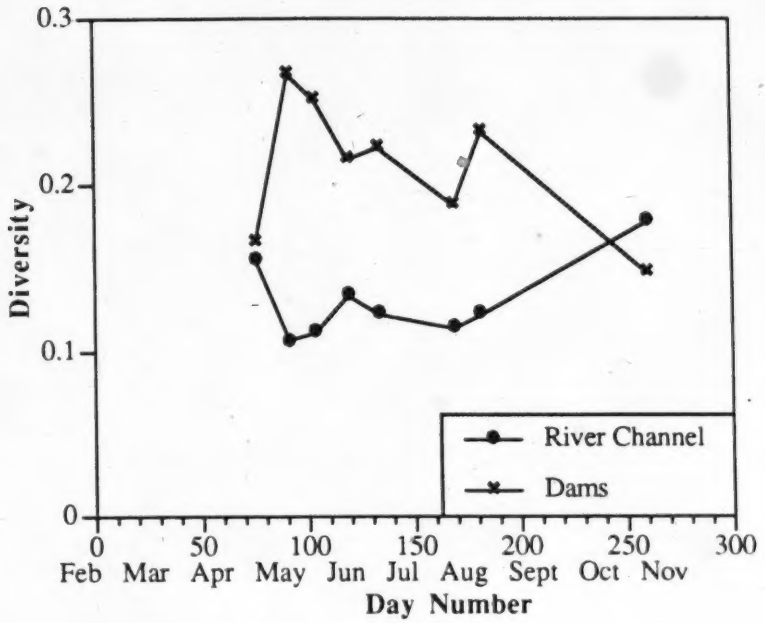


Figure 4. Faunal diversity on dams #1 and #2 and in the river channel between dams, 1986.

Dam #1: $f(x) = 53598.786x - 2769.832$, $r^2 = 0.188$
$F = 3.475$, $p = 0.082$, $n = 17$

Dam #2: $f(x) = 15361.06x + 3424.178$, $r^2 = 0.016$
$F = 0.279$, $p = 0.604$, $n = 19$

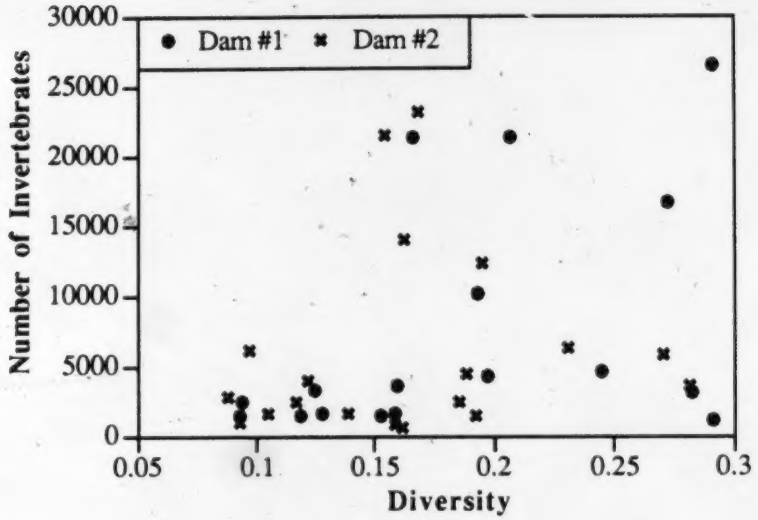
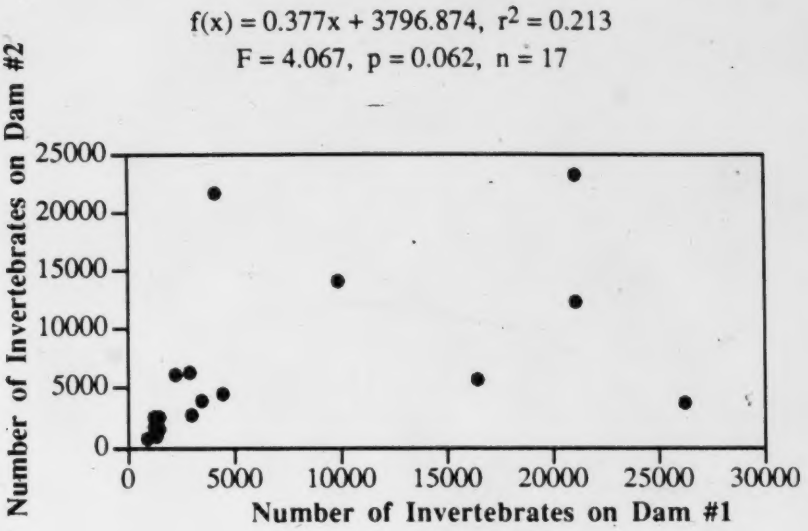


Figure 5. Average number of invertebrates per sample plotted against faunal diversity on dams #1 and #2, 1989.

A.



B.

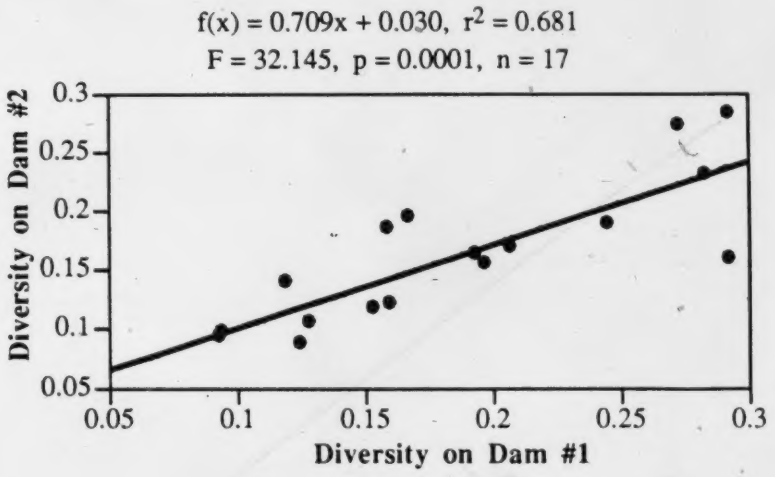


Figure 6. A. Average number of invertebrates per sample on dam #1 plotted against average number of invertebrates per sample on dam #2, 1989.

B. Faunal diversity on dam #1 plotted against faunal diversity on dam #2, 1989.

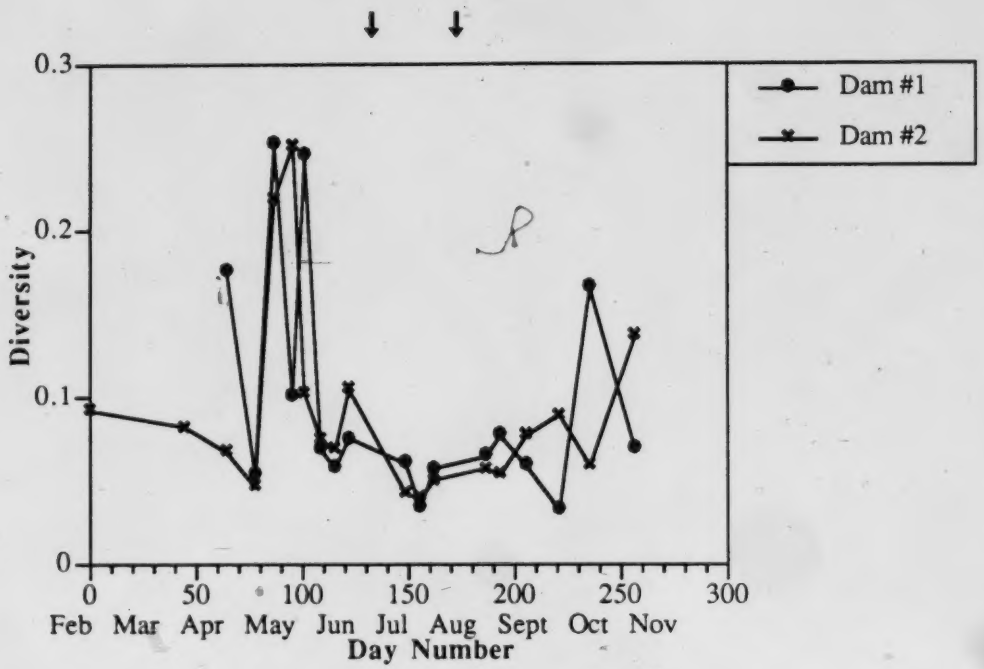


Figure 7 Faunal diversity excluding Chironomidae and Simuliidae on dams #1 and #2, 1989. Arrows correspond to the dates of floods in the river.

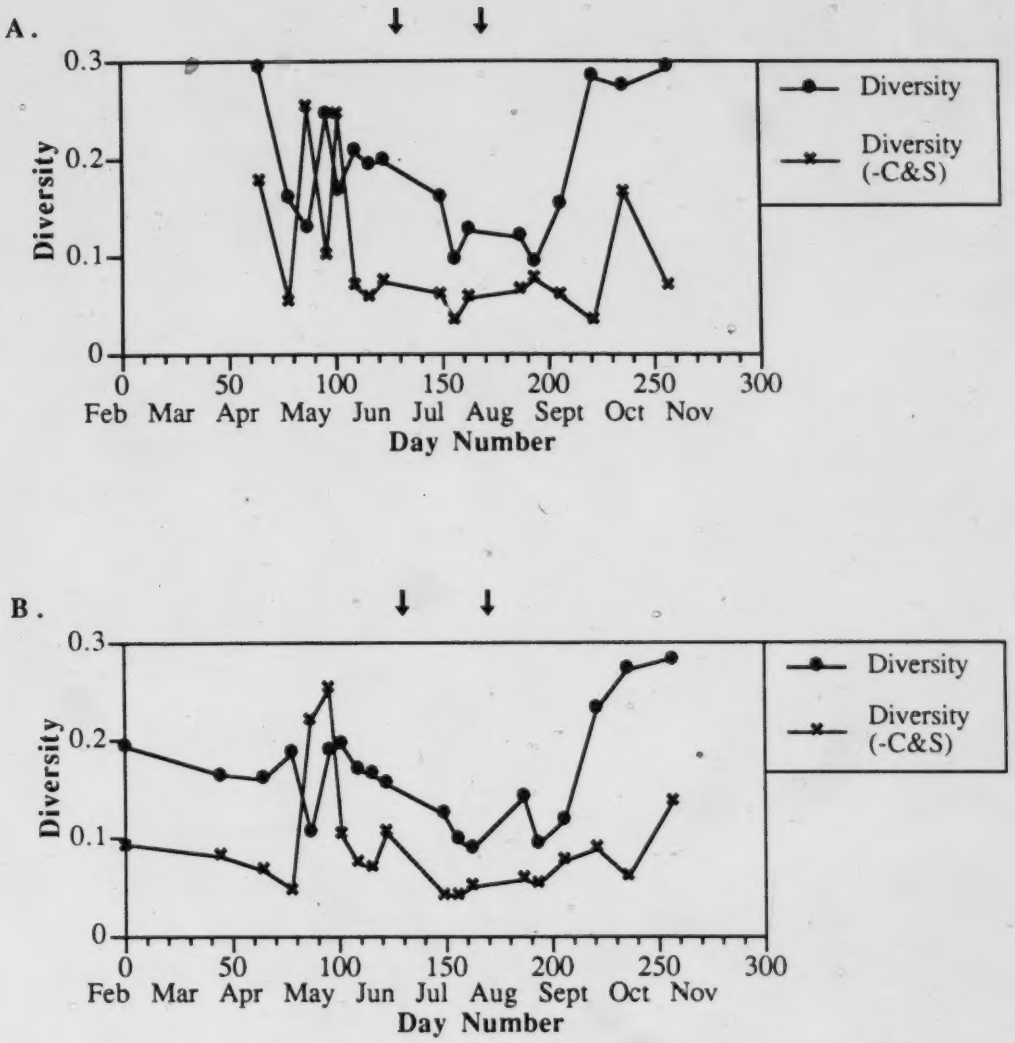


Figure 8. A. Total faunal diversity and diversity excluding Chironomidae and Simuliidae on dam #1, 1989.

B. Total faunal diversity and diversity excluding Chironomidae and Simuliidae on dam #2, 1989. Arrows correspond to the dates of floods in the river.

Community Composition

For purposes of analysis, I split the many taxa found on each beaver dam into 3 groups (Tables 1 and 2). This was done on the basis of overall percent composition of each taxon during the 1989 sampling season. An obvious first group (group 1) for both dams consisted of chironomids and simuliids, which made up between 30% and 60% of the total number of macroinvertebrates in the samples. The next most common taxon, the mayfly *Baetis* sp., accounted for only 1.4 to 2.7% on dams #1 and #2 respectively. It was more difficult to find cut-off points to group *Baetis* and the remaining taxa. I therefore decided to exclude Chironomidae and Simuliidae from my data set and recalculate percent composition for all remaining taxa. *Baetis* now accounted for 22% to 27% of the newly calculated total. *Baetis* and the next 12 taxa selected in this way constitute group 2. The remaining invertebrates collectively made up less than 1.5% of the total number (excluding Chironomidae and Simuliidae) and were placed in group 3. The taxon composition in groups 2 and 3 varied slightly between dams #1 and #2.

Frequency graphs were prepared for the 3 groups and for each taxon in groups 1 and 2 (Figures 9 – 16). For purposes of comparison between dams, a few taxa from group 3 were also included in these graphs; e.g. *Paraleptophlebia* sp. belongs to group 3 in dam #2. Each graph shows the percent of selected taxa for each sampling date on either dam #1 or dam #2 during 1989. The two arrows at the top of each graph indicate the two periods of high water in the river when samples could not be taken (29 June and 9 August or day numbers 129 and 170). Days are counted from the first sample taken: day number 1 denotes 20 February 1989 and day number 255 denotes 3 November 1989.

Chironomidae and Simuliidae were much more common than any other taxa. These two taxa made up more than 80% of the total number of invertebrates for most of the sampling season and showed only a slight decrease in relative abundance in late summer when other taxa increased in numbers. In terms of numbers, however, chironomid and

simuliid larvae were abundant throughout the collecting period (Tables 3 and 4). Simuliidae showed a marked decrease after each period of very high water and were most numerous throughout the summer (Figure 10). Chironomids, conversely, were the most important faunal component during the winter (Figure 10). Chironomids also decreased after floods.

It is important to keep in mind that invertebrate percentages graphed for group 2 are calculated excluding group 1 values except where the group is compared directly to both groups 1 and 3. For dam #1, group 2 is largely composed of invertebrates that reach their peak in numbers in summer, especially Plecoptera and Trichoptera.

Percentage composition of *Amphinemura* sp. (Plecoptera) peaked in late August and September, but *Amphinemura* was also present in high numbers on dam #2 in the February and April samples (Tables 3 and 4, and Figure 12). This early peak presumably represents over-wintering larvae.

It was also difficult to differentiate between early instars of *Hydropsyche* and *Cheumatopsyche*, as identification of these trichopteran larvae depends on certain thoracic sclerites, which are too lightly scleritised in small individuals to distinguish. Thus, small Hydropsychidae are included on the graphs of the two genera (Figure 13). Larvae of early instars reached their highest level in July and August and were replaced by larger larvae from July to September. Peaks for larvae of both genera were similar, and dam #2 data possibly reflect the flood that occurred in August, with a slight dip in trichopteran abundance in subsequent samples. There was also evidence of larger over-wintering *Hydropsyche* and *Cheumatopsyche* on dam #2.

Trends in the abundances of Ephemeroptera larvae were not clear (Figure 11). *Baetis* sp. appeared to have three peaks from May to September on each dam. *Paraleptophlebia* sp. larvae reached maximum relative abundance in September but *Paraleptophlebia* larvae were also present during winter.

Hydracarina specimens were most abundant during May, June and July, with a large peak of (60% of the total fauna [-C&S]) on dam #1 in May (Figure 14).

Mermithid nematodes, parasitic in Simuliidae, not surprisingly tended to follow larval simuliid abundance whilst within their host (Figure 15). Briefly, their life cycle involves the penetration of an early instar host, such as a black fly larva, by the free-living nematode, then development, and eventually emergence from the adult simuliid or the last larval instar simuliid. Emergence kills the host (Bailey *et al.* 1977, Colbo and Potter 1980). Mermithidae relative abundances correlated with those of the simuliids, peaking in late May/early June and again in July. The free-living stages were commonest in early June and disappeared in September. In Figure 16, the parasites' abundance is expressed as a percent of the black flies present and indicates that free-living mermithids were most abundant relative to their host in the early spring (February) and reappeared in low numbers in June and July. Mermithids were found in Simuliidae throughout the sampling season but reached their highest relative level in the summer (May to September).

Table 1. Total number of invertebrates and percent of total invertebrates for each taxon during 1989 on dam #1. [redacted] immature except those indicated as A = adult. Taxa representing less than 0.1% of the total are shown as 0%.

	Taxon	Number	%	% (minus Group I)	
1	Chironomidae	70762	57.4		Group I
2	Simuliidae	46128	37.4		
3	*Baetis*	1755	1.4	27.1	Group II
4	Hydracarina	1191	1	18.4	
5	Mermithidae in Simuliidae	616	0.5	9.5	
6	Small Ephemëroptera	501	0.4	7.7	
7	Oligochaeta	394	0.3	6.1	
8	*Amphinemura*	393	0.3	6.1	
9	Small Hydropsychidae	262	0.2	4	
10	*Cheumatopsyche*	188	0.2	2.9	
11	*Hydropsyche*	186	0.2	2.9	
12	Free-living Mermithidae	158	0.1	2.4	
13	*Paraleptophlebia*	142	0.1	2.2	
14	Small Plecoptera	135	0.1	2.1	
15	*Hydroptila*	117	0.1	1.8	Group III
16	Ceratopogonidae	90	0.1	1.4	
17	Tipulidae	76	0.1	1.2	
18	Plecoptera/Ephemeroptera	55	0	0.8	
19	*Hyalella azteca*	48	0	0.7	
20	Nematoda	48	0	0.7	
21	*Caenis*	26	0	0.4	
22	*Pericoma*	15	0	0.2	
23	Limnephilidae	15	0	0.2	
24	Corixidae	15	0	0.2	
25	*Pisidium*	15	0	0.2	
26	*Agabus*	11	0	0.2	
27	*Lepidostoma*	6	0	0.1	
28	*Physa*	5	0	0.1	
29	*Stenacron*	2	0	0	
30	Odonata	2	0	0	
31	Hemiptera (Terrestrial)	2	0	0	
32	*Stenonema*	1	0	0	
33	*Brachycentrus*	1	0	0	
34	*Rhyacophila*	1	0	0	
35	Trichoptera	1	0	0	
36	*Agabus* (A)	1	0	0	
37	Elmidae (A)	1	0	0	
38	*Endalus* (A)	1	0	0	
39	*Amphizoa*	1	0	0	
40	Staphylinidae (A) (Terrestrial)	1	0	0	
41	Coleoptera	1	0	0	
42	*Aeshna*	1	0	0	
43	*Somatochlora*	1	0	0	
44	*Leucorrhinia*	1	0	0	
45	*Armiger crista*	1	0	0	
46	Limnaeidae	1	0	0	
47	Hirudinea	1	0	0	
48	Nematomorpha	1	0	0	
	Total on dam #1	123376			

Table 2. Total number of invertebrates and percent of total invertebrates for each taxon during 1989 on dam #2. All are immature except those indicated as P = pupae or A = adult. Taxa representing less than 0.1% of the total are shown as 0%.

	Taxon	Number	%	% (minus Group I)	
1	Simuliidae	63887	56.6		Group I
2	Chironomidae	35526	31.5		
3	*Baetis*	3082	2.7	22.8	Group II
4	Hydracarina	2374	2.1	17.6	
5	*Amphinemura*	2067	1.8	15.3	
6	Small Ephemeroptera	1702	1.5	12.6	
7	Mermithidae in Simuliidae	800	0.7	5.9	
8	Oligochaeta	725	0.6	5.4	
9	*Hydropsyche*	573	0.5	4.2	
10	Small Hydropsychidae	573	0.5	4.2	
11	Free-living Mermithidae	308	0.3	2.3	
12	*Cheumatopsyche*	271	0.2	2	
13	Nematoda	199	0.2	1.5	
14	Tipulidae	146	0.1	1.1	Group III
15	*Paraleptophlebia*	145	0.1	1.1	
16	Ceratopogonidae	99	0.1	0.7	
17	*Agabus*	76	0.1	0.6	
18	*Hydroptila*	63	0.1	0.5	
19	*Pisidium*	56	0	0.4	
20	*Pericoma*	51	0	0.4	
21	*Caenis*	32	0	0.2	
22	Thysanoptera (Terrestrial)	25	0	0.2	
23	*Hyalella azteca*	22	0	0.2	
24	Corixidae	10	0	0.1	
25	Trichoptera	9	0	0.1	
26	Staphylinidae (A) (Terrestrial)	8	0	0.1	
27	*Rhyacophila*	7	0	0.1	
28	*Lepidostoma*	7	0	0.1	
29	*Physa*	6	0	0	
30	Hirudinea	4	0	0	
31	*Agabus* (A)	3	0	0	
32	Limnephilidae (Menotaulius?)	3	0	0	
33	*Brachycentrus*	3	0	0	
34	Limnaeidae	3	0	0	
35	Planorbidae	3	0	0	
36	Homoptera (Terrestrial)	3	0	0	
37	*Oecetis*	2	0	0	
38	*Somatochlora*	2	0	0	
39	*Gyrinus*	2	0	0	
40	*Pericoma* (P)	1	0	0	
41	*Ephemera*	1	0	0	
42	Small Plecoptera	1	0	0	
43	Unidentified Plecoptera/Ephemeroptera	1	0	0	
44	*Aeshna*	1	0	0	
45	*Brychius*	1	0	0	
46	*Brychius* (A)	1	0	0	
47	Dytiscidae, sp 1 (A)	1	0	0	
48	*Endalus* (A)	1	0	0	
49	Gyrinidae (A)	1	0	0	
50	*Haliplus* (A)	1	0	0	

Table 2, continued.

	Taxon	Number	Percent	Percent (minus Group I)
51	Dytiscidae, sp 2 (A)	1	0	0
52	Elmidae (A)	1	0	0
53	Coleoptera (A)	1	0	0
54	Hemiptera	1	0	0
55	Carabidae (A) (Terrestrial)	1	0	0
56	Nematodes in Chironomidae	1	0	0
57	Nematomorpha	1	0	0
58	Tardigrada	1	0	0
59	Ichneumenidae (Terrestrial)	2	0	0
60	Formicidae (Terrestrial)	2	0	0
61	Araneidae (Terrestrial)	1	0	0
	Total on dam #2	112901		

Table 3. Average number of animals on dam #1 per sampling date, 1989.

Date	Chironomidae	Simuliidae	Small Ephemeroptera	*Baetis*	*Paraleptophlebia*	*Amphinemura*
25-Apr	900	4	0	0	8	1
8-May	977	482	0	0	3	0
17-May	319	184	0	0	0	0
26-May	253	4074	104	0	0	0
1-Jun	14825	5326	10	917	0	0
8-Jun	2823	17352	224	270	4	17
15-Jun	1657	7792	0	149	0	0
22-Jun	612	3325	2	59	0	10
18-Jul	748	2443	0	44	0	13
25-Jul	1073	655	86	84	0	45
1-Aug	716	1853	73	154	1	18
25-Aug	269	717	1	11	6	79
1-Sep	344	661	2	15	9	150
13-Sep	898	102	0	41	40	55
29-Sep	2833	66	0	2	4	0
13-Oct	15691	758	0	3	36	0
3-Nov	25829	337	0	8	32	6
Total	70762	46128	1755	1191	616	501
Total Percent	57.4	37.4	1.4	1.0	0.5	0.4

Date	Small Hydropsychidae	*Cheumatopsyche*	*Hydropsyche*	Hydracarina	Mermithidae in Simuliidae	Free-living Mermithidae
25-Apr	0	0	0	0	0	0
8-May	0	0	0	12	0	0
17-May	0	0	0	886	0	0
26-May	0	0	0	7	21	0
1-Jun	0	0	0	9	4	0
8-Jun	0	0	0	20	316	117
15-Jun	0	0	0	88	94	27
22-Jun	0	0	1	100	23	9
18-Jul	68	6	7	25	111	3
25-Jul	47	14	44	17	33	0
1-Aug	145	13	41	17	13	2
25-Aug	0	57	56	3	3	0
1-Sep	1	84	23	2	0	0
13-Sep	1	16	13	3	0	0
29-Sep	0	0	1	0	0	0
13-Oct	0	0	0	0	0	0
3-Nov	0	0	0	4	0	0
Total	394	393	262	188	186	158
Total Percent	0.3	0.3	0.2	0.2	0.2	0.1

Table 4. Average number of animals on dam #2 per sampling date, 1989.

Date	Chironomidae	Simuliidae	Small Ephemeroptera	*Baetis*	*Paraleptophlebia*	*Amphinemura*
20-Feb	1079	2	0	0	7	144
5-Apr	334	0	0	0	0	57
25-Apr	572	8	0	2	4	3
8-May	1718	575	0	1	2	0
17-May	389	682	300	0	7	0
26-May	282	3372	649	0	2	0
1-Jun	830	9660	335	805	0	12
8-Jun	4636	16464	8	740	0	319
15-Jun	2288	9888	16	424	0	392
22-Jun	3884	14680	32	512	0	392
18-Jul	914	2202	75	64	0	55
25-Jul	1695	2867	257	267	0	153
1-Aug	700	1196	29	140	0	62
25-Aug	307	942	0	17	2	42
1-Sep	398	134	2	22	7	67
13-Sep	1391	335	0	61	3	274
29-Sep	5398	604	0	30	94	34
13-Oct	5288	231	0	0	9	21
3-Nov	3427	49	0	0	11	43
Total	35526	63887	1702	3082	145	2067
Total Percent	31.5	56.6	1.5	2.7	0.1	1.8

Date	Small Hydropsychidae	*Cheumatopsyche*	*Hydropsyche*	Hydracarina	Mermithidae in Simuliidae	Free-living Mermithidae
20-Feb	0	10	7	0	0	0
5-Apr	0	5	0	0	0	0
25-Apr	0	0	0	0	0	0
8-May	0	0	0	7	0	0
17-May	0	1	0	13	0	0
26-May	0	0	0	4	6	0
1-Jun	0	0	0	21	333	0
8-Jun	4	0	0	230	128	256
15-Jun	0	0	0	510	28	13
22-Jun	4	0	0	1472	74	20
18-Jul	134	6	64	32	141	9
25-Jul	221	71	129	37	61	6
1-Aug	187	64	148	14	18	4
25-Aug	8	24	74	5	11	0
1-Sep	2	31	50	5	0	0
13-Sep	15	60	100	4	0	0
29-Sep	0	0	2	14	0	0
13-Oct	0	0	0	9	0	0
3-Nov	0	0	0	0	0	0
Total	573	271	573	2374	800	308
Total Percent	0.5	0.2	0.5	2.1	0.7	0.3

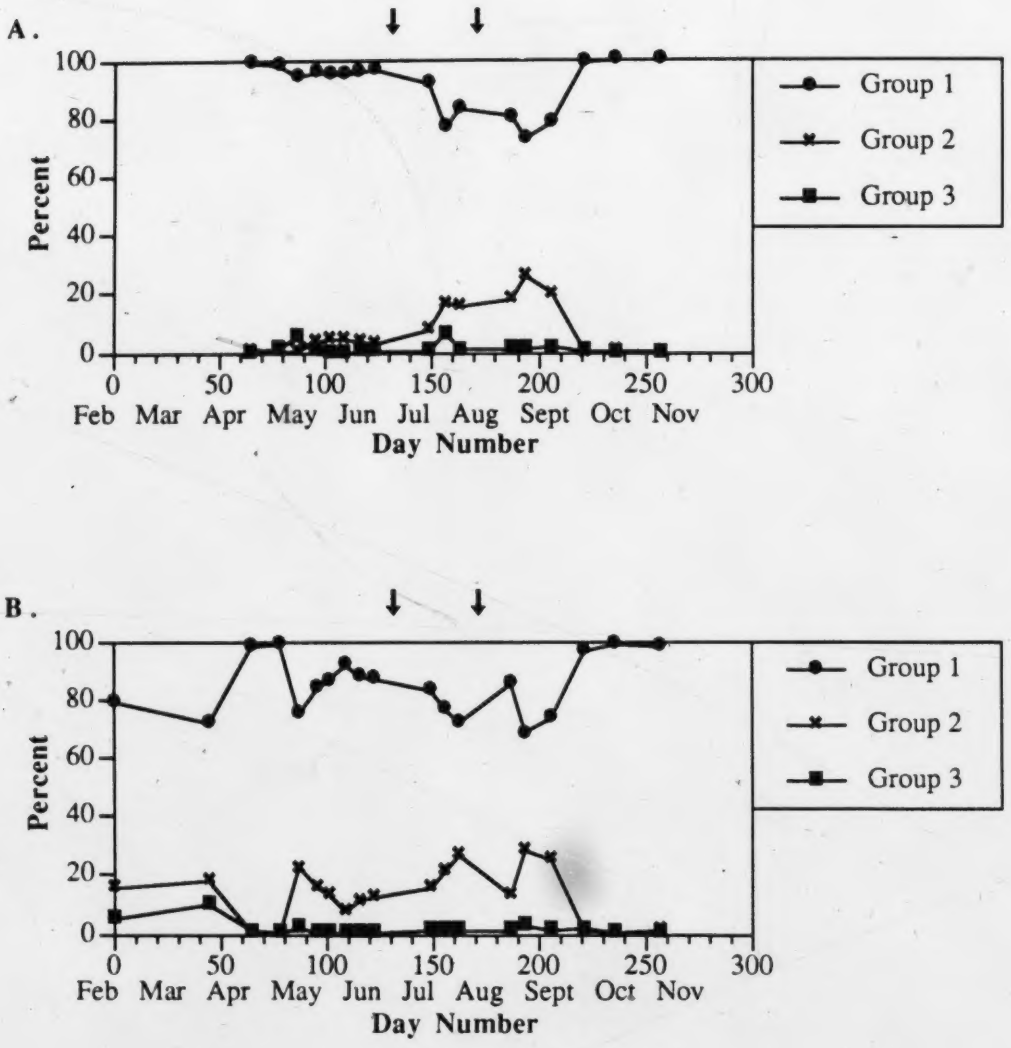


Figure 9. Percent of taxonomic Groups 1, 2 and 3 on dam #1 (A) and dam #2 (B) in the Bigoray River, 1989. Arrows correspond to the dates of floods in the river.

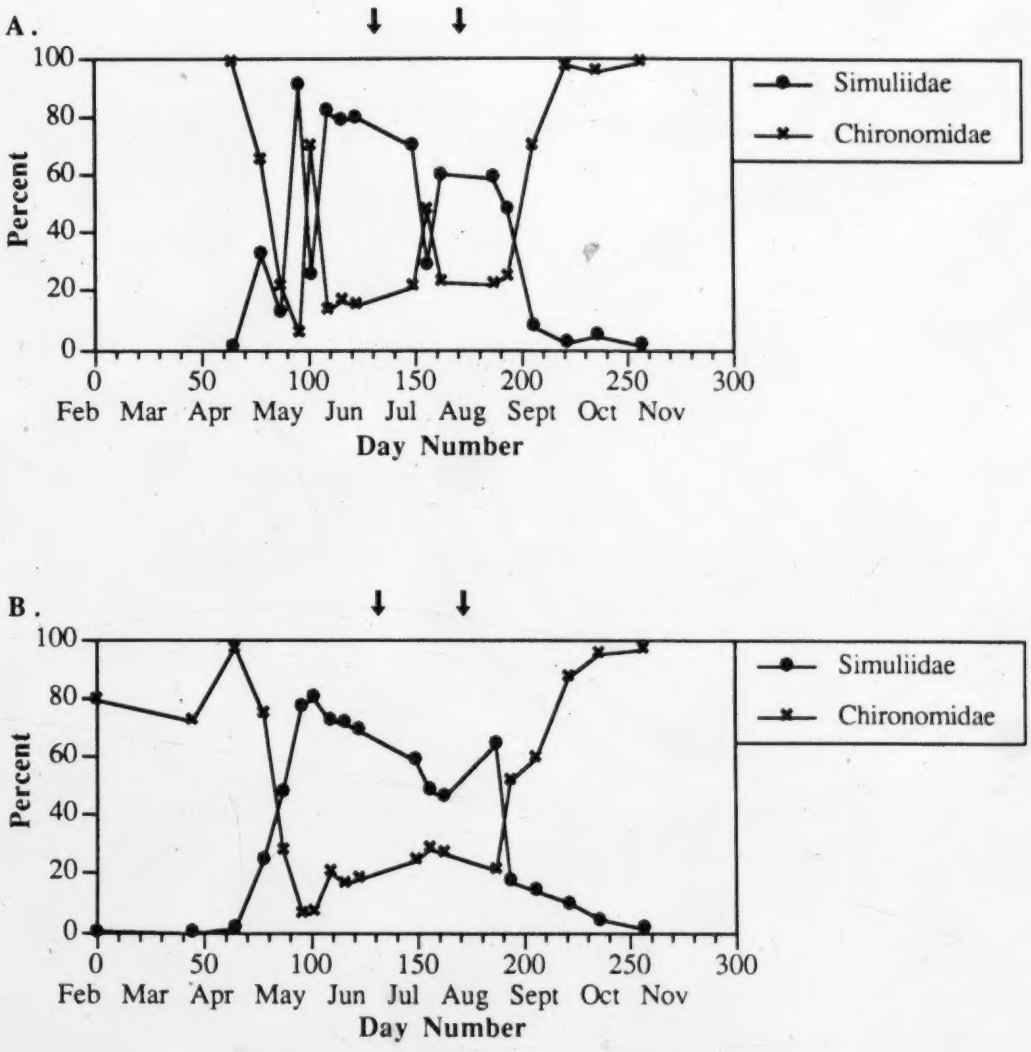


Figure 10. Percent of Simuliidae and Chironomidae (group 1) on dam #1 (A) and dam #2 (B) in the Bigoray River, 1989. Arrows correspond to the dates of floods in the river.

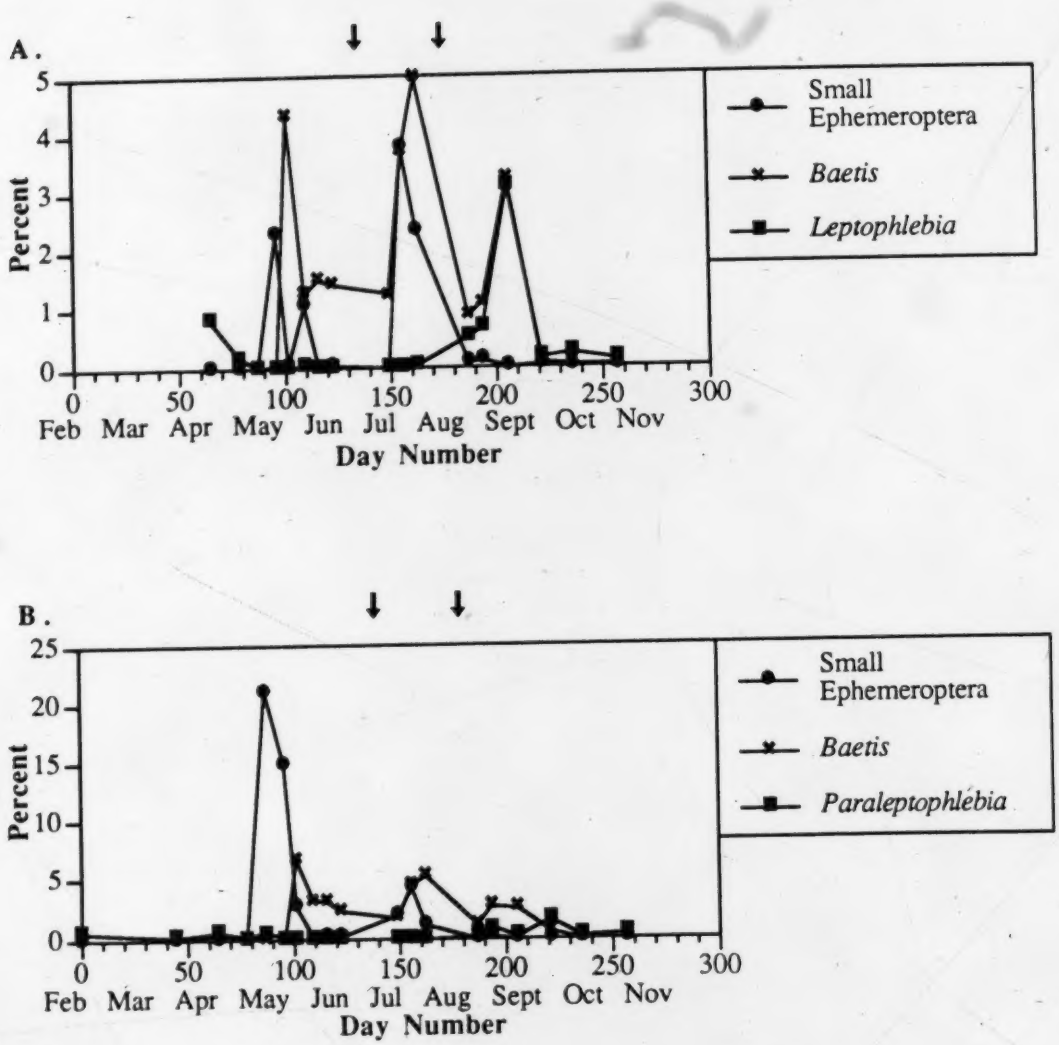


Figure 11. Percent of Ephemeroptera (excluding Chironomidae and Simuliidae) on dam #1 (A) and dam #2 (B) in the Bigoray River, 1989. Arrows correspond to the dates of floods in the river.

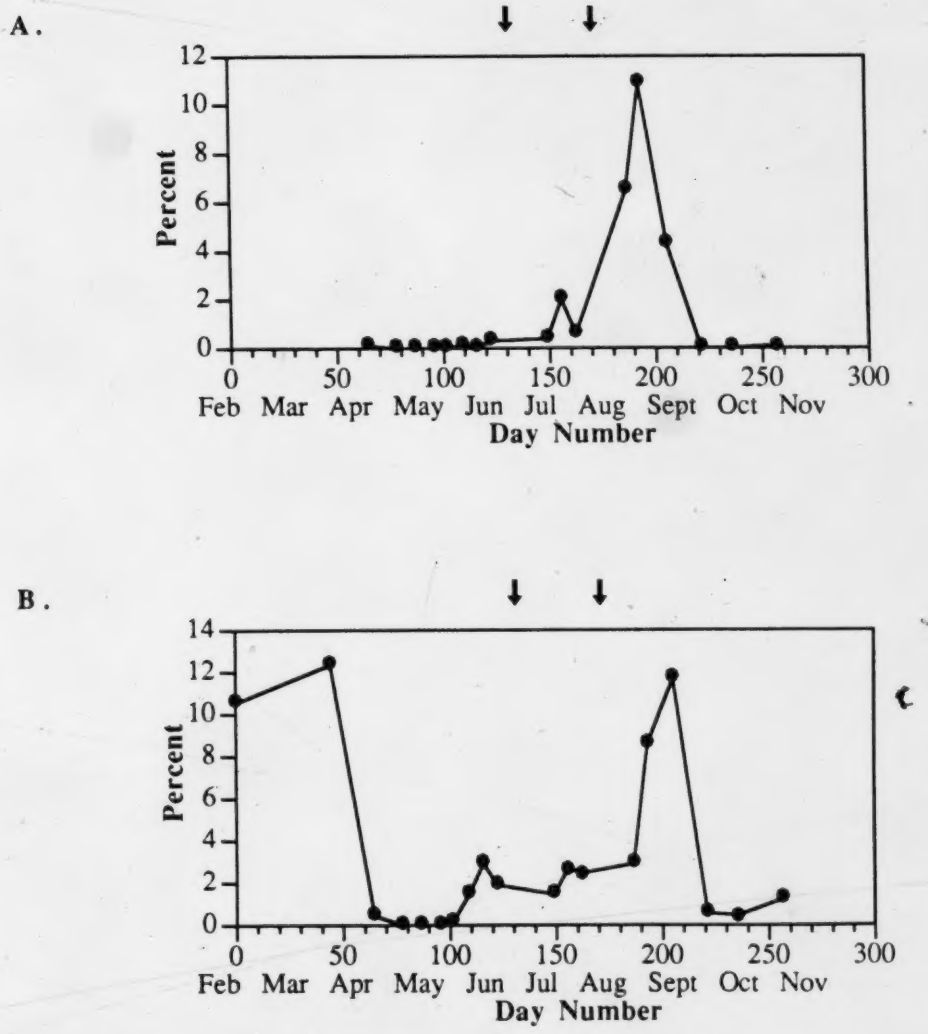


Figure 12. Percent of *Amphinemura* (Plecoptera) (excluding Chironomidae and Simuliidae) on dam #1 (A) and dam #2 (B) in the Bigoray River, 1989. Arrows correspond to the dates of floods in the river.

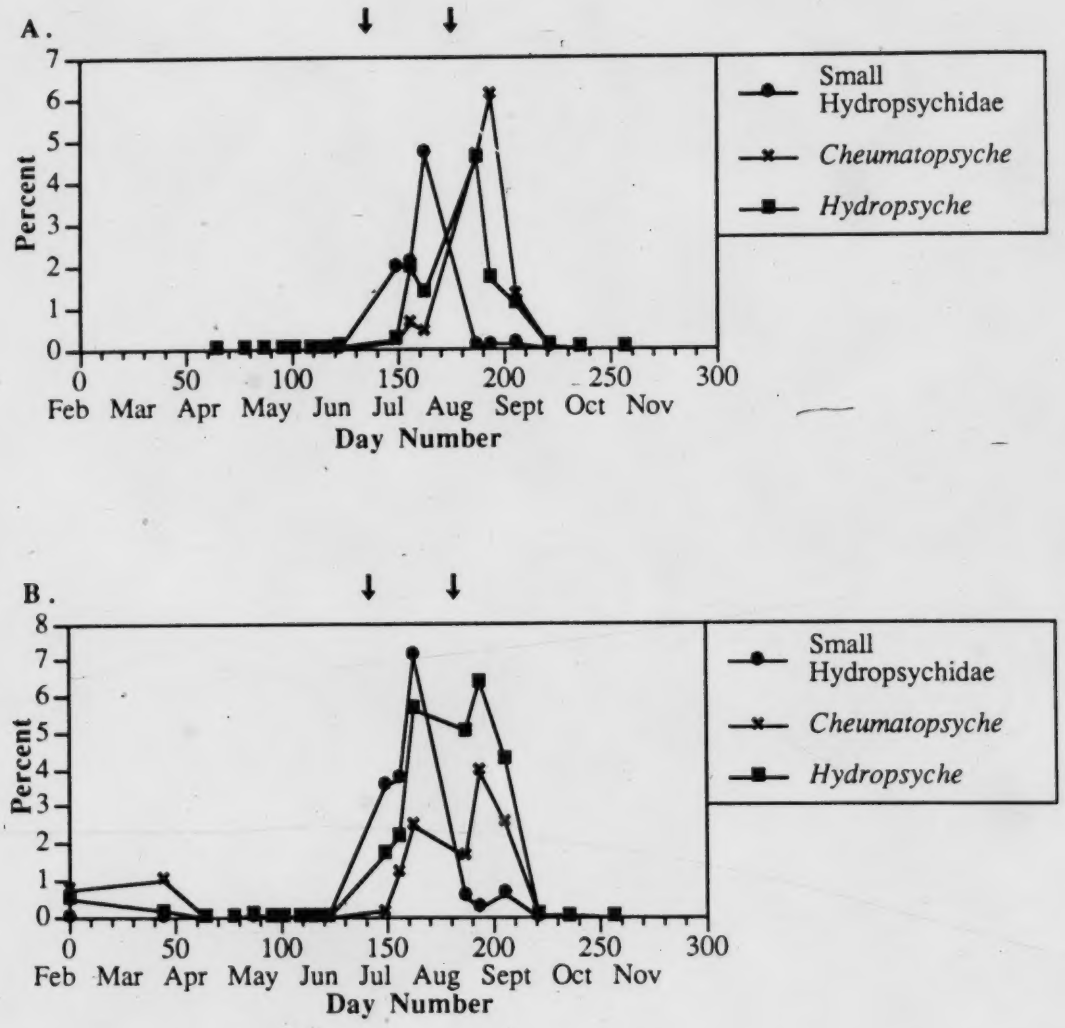
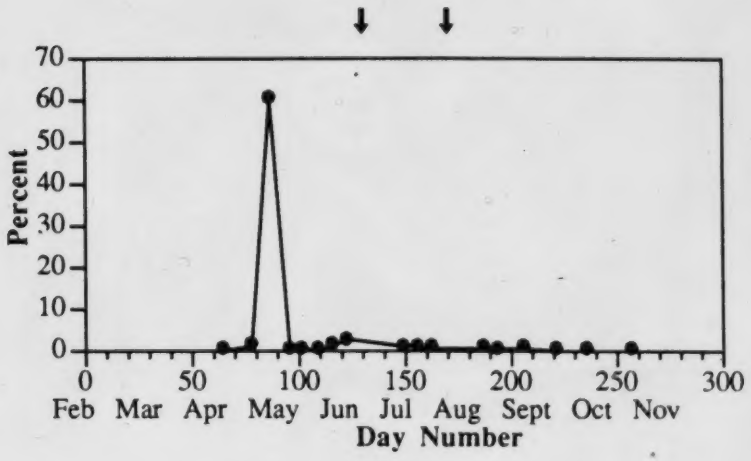


Figure 13. Percent of Trichoptera (excluding Chironomidae and Simuliidae) on dam #1 (A) and dam #2 (B) in the Bigoray River, 1989. Arrows correspond to the dates of floods in the river.

A.



B.

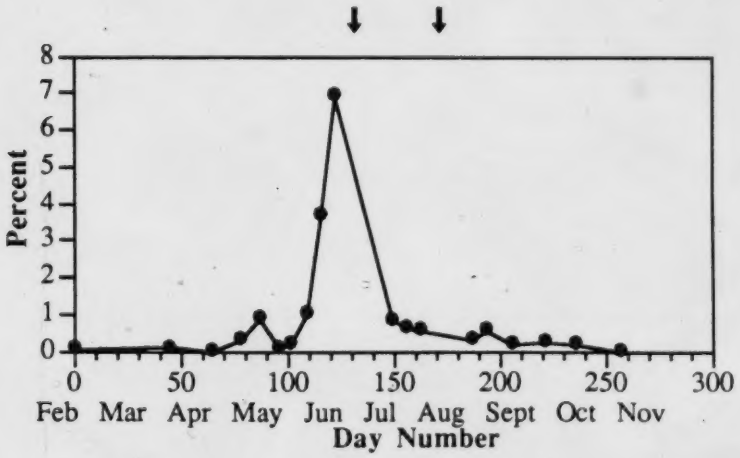


Figure 14. Percent of Hydracarina (excluding Chironomidae and Simuliidae) on dam #1 (A) and dam #2 (B) in the Bigoray River, 1989. Note that the scale of percent on graph A is 0-70, and that on graph B is 0-8. Arrows correspond to the dates of floods in the river.

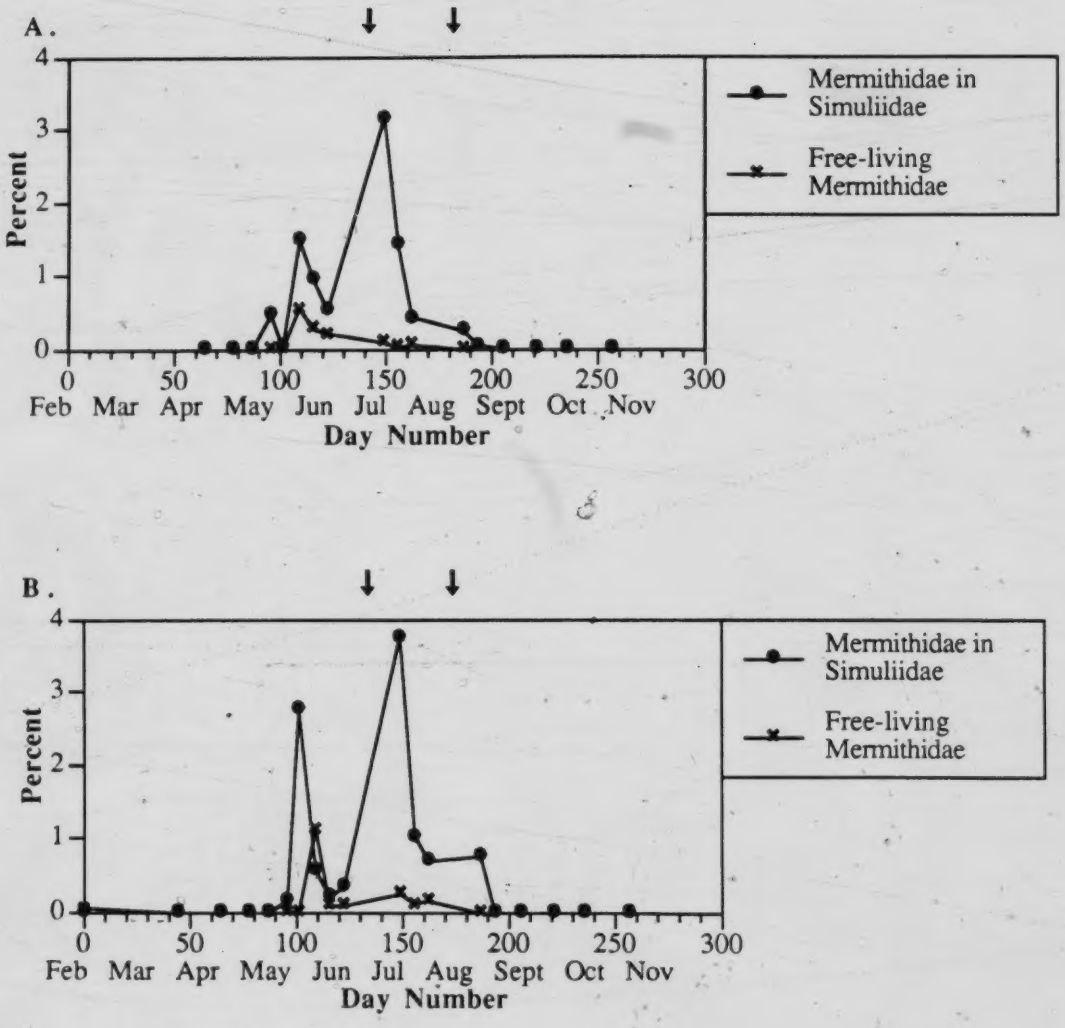


Figure 15. Percent of Mermithidae (excluding Chironomidae and Simuliidae) on dam #1 (A) and dam #2 (B) in the Bigoray River, 1989. Arrows correspond to the dates of floods in the river.

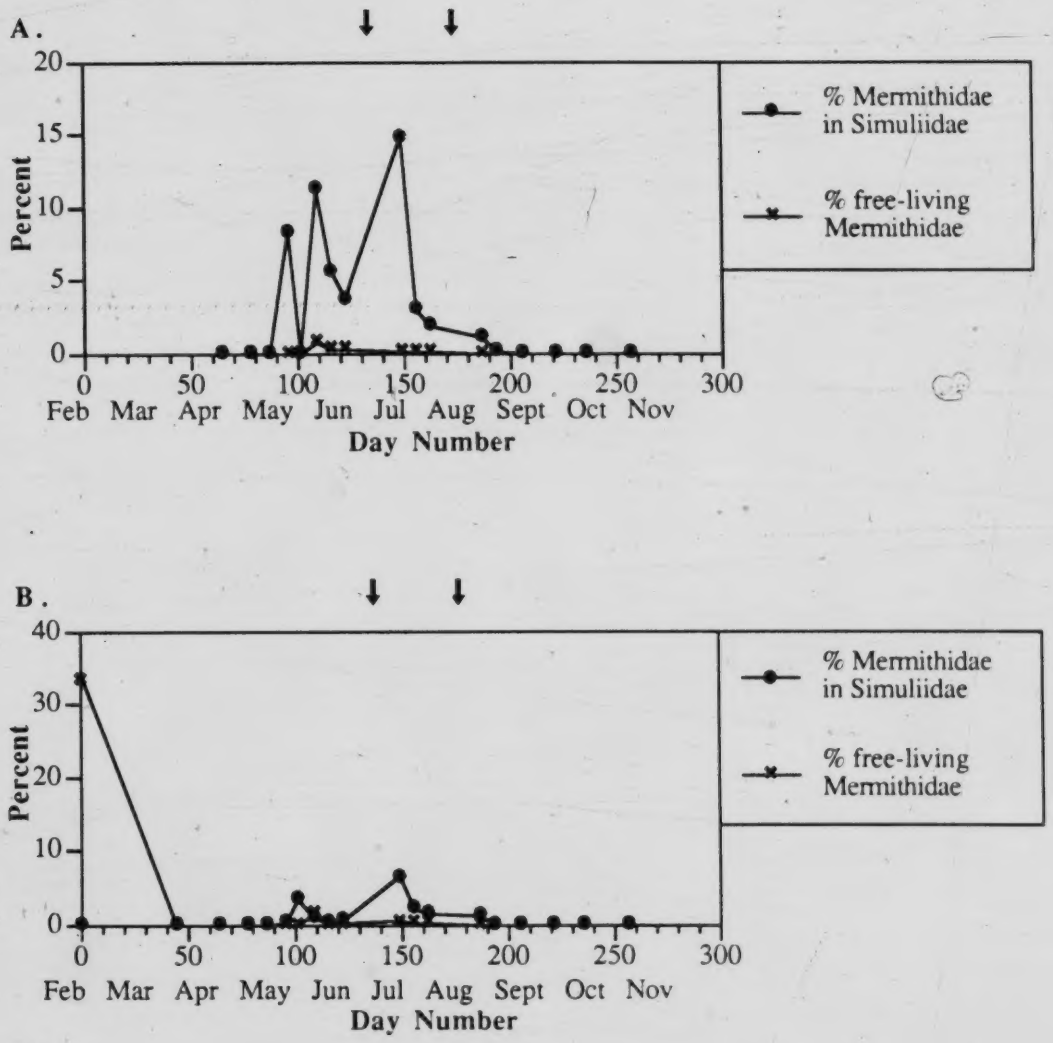


Figure 16. Percent of Simuliidae infected by Mermithidae, and free-living Mermithidae as a percent of Simuliidae present on dam #1 (A) and dam #2 (B) in the Bigoray River, 1989. Arrows correspond to the dates of floods in the river.

Trophic relationships and habitats of aquatic invertebrates associated with beaver dams.

(Tables 5 and 6; also Appendix 2).

Aquatic invertebrates collected from beaver dams live in a variety of micro-habitats found on the dams. The habitats from which previous workers have collected these animals, and the trophic relationships of the taxa I studied, illustrate that the beaver dam per se can be a complex and diverse faunal environment. I discuss the taxa collected in 1989 in terms of their feeding habits and preferred habitat (as reported in the literature). Insect orders containing especially numerous or unusual genera are treated separately, and then the remaining insects and non-insect taxa are discussed.

Diptera. Dudley and Anderson (1982) suggest that dipterans are the major wood decomposers in aquatic habitats because they burrow in soft wood. However, except for perhaps some chironomids and tipulids, none of the dipterans collected from the dams were burrowers in wood. Chironomids and simuliids were by far the most numerous invertebrates found on the dams, but they reportedly use the wood mainly as a substrate (Chironomidae) and for attachment (Simuliidae). *Pericoma* (Psychodidae) burrows in detritus and is best suited to lentic or lotic-depositional habitats. Pereira *et al.* (1982) found fungi in the gut of *Pericoma*, but no wood.

Ephemeroptera. The mayflies on the dams in the Bigoray River feed mostly by scraping and collecting. *Paraleptophlebia* and *Baetis* were abundant on dams, second only in total abundance to simuliids and chironomids. Larvae of 2 other mayfly genera, *Ephemera* and *Caenis*, are characteristic of depositional regions of rivers and lakes. Small numbers of heptageniids were also present. Pereira *et al.* (1982) found wood in the guts of most wood-dwelling ephemeropterans examined, but wood was less important in their

diet than components of the aufwuchs layer. *Baetis* was common on wood of the dams, but Pereira *et al.* (1982) found *Baetis* larvae to be equally common on other suitable substrates. Pereira *et al.* (1982) found *Paraleptophlebia* larvae on wood in backwaters or on rotten wood and found large amounts of wood in the guts of the larvae.

Plecoptera. Larvae of *Amphinemura*, a detritivore, were numerous on dams. Larvae appeared to live in detritus trapped by the dam rather than on the wood, unless the wood was in an advanced state of decay. A few specimens of the predator *Isoperla* were also found. Predators tend to use wood as a habitat, and indeed only trace amounts of wood were found by Pereira *et al.* (1982) in the guts of most stoneflies, even detritivores.

Trichoptera. Trichoptera larvae, in terms of feeding habits, were probably the most diverse group of insects found in beaver dams. The order contained genera representing predators, collectors-gatherers, collector-filterers, scrapers, and shredders. Most taxa prefer erosional habitats, although some larvae also tolerate depositional environments. Hydropsychids use the wood as substrate and to suspend nets for feeding. *Lepidostoma* and several genera of Limnephilidae, considered by Dudley and Anderson (1982) to be closely associated with wood, use the wood for feeding, case-making and pupation. *Rhyacophila* were fairly common predators on the dams. In all, 16 out of 25 caddis genera examined by Pereira *et al.* had wood in their gut, and as these animals are relatively large, it is possible that they have a significant effect on the degradation of wood in the dams.

Coleoptera. Larval and adult beetles, although a diverse group, were a minor component of the dam fauna. *Agabus* was the most numerous beetle taxon found. The larvae are predators that pierce their prey. They are tolerant of several habitat types

including lotic-erosional and lotic-depositional. Other coleopterans represented shredders, scavengers, scrapers, and predators, and both adults and larvae can be found in many kinds of aquatic and semi-terrestrial habitats.

Mollusca. Molluscs on dams tended to be either filter feeding bivalves (*Pisidium*) that prefer soft lake and stream bottoms or omnivorous gastropods (e.g. *Physa*) often associated with vegetation and detritus.

Others. Hydracarina, normally associated with vegetation, were well represented on dams. Larvae, nymphs and adults tend to pierce and suck the fluids from their prey. One gammarid (Crustacea), *Hyalella*, was frequently collected. It is a scavenger, common in both lentic and lotic environments. A few odonate specimens were collected; they are all predators. Other rare taxa include Hirudinea (carnivores, detritivores or blood-suckers), Nematomorpha (non-feeding as adults and normally restricted to shallow, slow-moving water or ponds), Tardigrada (moss- or plant-dwellers), nematodes, and oligochaetes. These latter two taxa are detritivores, but nematodes occur in all sorts of aquatic habitats and can also be herbivorous, predatory, or parasitic.

Table 5. Numbers and trophic relationships of aquatic invertebrates found in beaver dams of the Bigoray River. Numbers in parenthesis = number of taxa. See note at bottom of page for explanation of feeding terms. (Sources: Merritt and Cummins 1978, Pennak 1978)

Collectors-gatherers (15)	Collectors-filterers (6)	Piercers-herbivores (5)	Piercers-predators (6)	Scrapers (9)
Chironomidae	Chironomidae	*Hydroptila*	Chironomidae	*Baetis*
Tipulidae	Simuliidae	*Brychius*	*Agabus*	*Caenis*
Ceratopogonidae	*Hydropsyche*	*Haliplus*	Dytiscidae, sp 1	*Stenacron*
Pericoma	*Cheumatopsyche*	Corixidae	Dytiscidae, sp 2	*Stenonema*
Baetis	*Brachycentrus*	Tardigrada	Corixidae	*Hydroptila*
Caenis	*Pisidium*		Hydracarina	Limnephilidae
Paraleptophlebia				*Brachycentrus*
Stenacron				*Brychius*
Stenonema				Elmidae
Ephemera				
Amphinemura				
Isoperla				
Rhyacophila				
Limnephilidae				
Elmidae				

Shredders-herbivores (3)	Shredders-detritivores (5)	Scavengers-detritivores (6)	Engulfers-predators (13)	Do not feed (1)
Oecetis	Tipulidae	*Gyrinus*	Chironomidae	Nematomorpha
Endalus	*Paraleptophlebia*	*Hyalella*	Ceratopogonidae	
Haliplus	*Amphinemura*	*Physa*	*Rhyacophila*	
	Lepidostoma	Hirudinea	*Oecetis*	
	Limnephilidae	Oligochaeta	*Amphizoa*	
		Nematoda	*Gyrinus*	
			Staphylinidae	
			Corixidae	
			Somatochlora	
			Leucorrhinia	
			Aeshna	
			Hirudinea	
			Nematoda	

Note: General classification system for aquatic insect trophic relations (Merritt and Cummins 1978):

Collectors are detritivores that either filter fine particulate organic matter (FPOM) from the water or gather or deposit-feed on sediment or on the surface film. Piercers are either herbivores that pierce cells and tissues of living vascular hydrophytes and filamentous algae and suck fluids from them, or they are carnivores that pierce the cells and tissues of their prey. Scrapers feed on periphyton (attached algae and other material) by grazing hard surfaces. Shredders are either herbivores feeding on living vascular hydrophyte plant tissue or detritivores that chew or bore into decomposing vascular plant tissue or wood – coarse particulate organic matter (CPOM). Engulfers are carnivores, and consume whole animals or parts of them.

Table 6. Habitats of aquatic invertebrates found in beaver dams of the Bigoray River. Vasc = vascular; numbers in parenthesis = number of taxa found in a specified habitat (Sources: Merritt and Cummins 1978, Pennak 1978, Borrer *et al.* 1981).

Lotic - erosional (23)	Lotic - depositional (24)	Lotic - vasc hydrophytes (6)	Lentic - littoral (21)	Lentic - erosional (7)	Lentic - vasc hydrophytes (11)
Chironomidae	Chironomidae	*Brachycentrus*	Chironomidae	Chironomidae	*Agabus*
Simuliidae	Tipulidae	*Gyrinus* (L)	Tipulidae	*Stenacron*	*Endalus*
Tipulidae	Ceratopogonidae	Hydracarina	Ceratopogonidae	*Stenonema*	*Gyrinus* (L)
Baetis	*Pericoma*	*Hyalella*	*Pericoma*	*Hydropsyche*	*Haliplus*
Paraleptophlebia	*Baetis*	*Physa*	*Baetis*	Limnephilidae	Dytiscidae, sp 2
Stenacron	*Caenis*	Tardigrada	*Caenis*	*Brychius*	Corixidae
Stenonema	*Ephemera*		*Ephemera*	Nematoda	*Leucorrhinia*
Amphinemura	*Amphinemura*		Limnephilidae		Hydracarina
Isoperla	*Isoperla*		*Oecetis*		*Hyalella*
Hydropsyche	*Hydroptila*		Dytiscidae, sp 1		*Physa*
Cheumatopsyche	*Lepidostoma*		*Gyrinus* (A)		Tardigrada
Hydroptila	Limnephilidae		*Somatochlora*		
Rhyacophila	*Oecetis*		*Aeshna*		
Lepidostoma	*Agabus*		Hydracarina		
Limnephilidae	*Gyrinus* (A)		*Pisidium*		
Brachycentrus	Corixidae		*Physa*		
Oecetis	*Somatochlora*		Hirudinea		
Agabus	*Aeshna*		Oligochaeta		
Amphizoa	*Pisidium*		Nematomorpha		
Brychius	*Physa*		Nematoda		
Elmidae	Hirudinea		Tardigrada		
Aeshna	Oligochaeta				
Nematoda	Nematomorpha				
	Nematoda				

Life History of *Pericoma kincaidi*

I used Quate's 1955 key to identify specimens of Psychodidae (Diptera). Those raised in the laboratory were *Pericoma kincaidi* Quate (in the *Pericoma bipunctata* complex). However, confirmation of this identification is required.

I sampled *P. kincaidi* on dams #1 and #2 from March to October 1988. Average number of larvae per sample was calculated from 1 to 8 samples (average number 4.6) taken from the dams on each sampling day. Although the samples taken were not strictly quantitative, I wanted to show mainly the presence or absence of certain larval instars, and considered average numbers to be a reasonable way of doing this.

The larvae peaked sharply in numbers in June and remained abundant until the end of August (Table 7 and Figure 17). However they were present throughout the year in low numbers. Larval head capsule width was measured for all larvae between April and August (Figure 18) Three size groupings could be distinguished from the results, and by raising and breeding *Pericoma* I determined that these represented second, third and fourth instar larvae. Only the largest instar larvae were collected in April and May. By the end of May, larvae of all 3 size classes had appeared on the dams, and from then until August the size distribution gradually shifted towards largest instar larvae.

Table 7 Number of samples, and total and average number of *Pericoma kincaidi* larvae collected per sampling date, 1988.

Date	Day	Number of Samples	Total *Pericoma*	Average *Pericoma*
8-Apr	1	1	10	10
26-Apr	19	5	53	11
16-May	39	2	3	2
27-May	50	5	10	2
9-Jun	63	3	0	0
20-Jun	74	4	236	59
4-Jul	88	4	420	105
14-Jul	98	5	443	89
25-Jul	109	5	212	42
8-Aug	123	5	306	61
23-Aug	138	4	8	2
7-Sep	153	7	6	1
27-Sep	173	6	10	2
17-Oct	193	8	32	4
Average		4.6		28

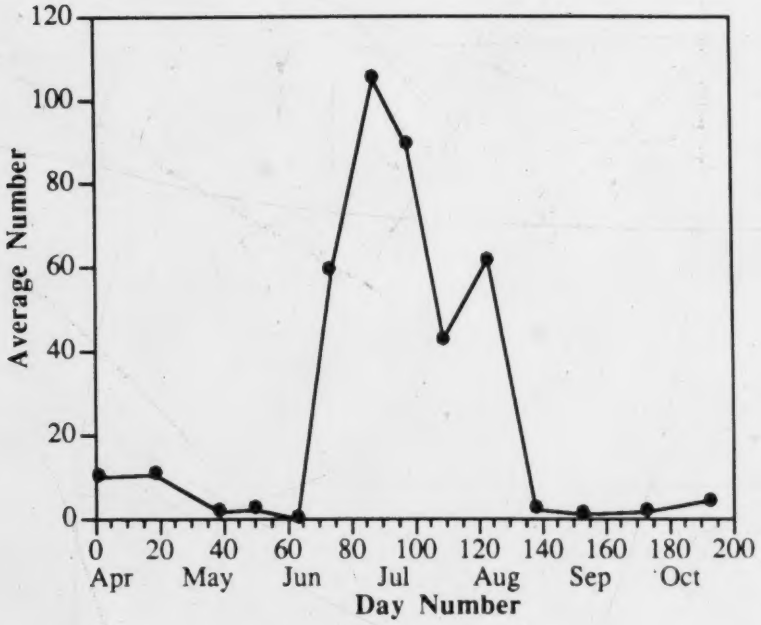


Figure 17. Average number of *Pericoma kincaidi* larvae in the Bigoray River, 1988.

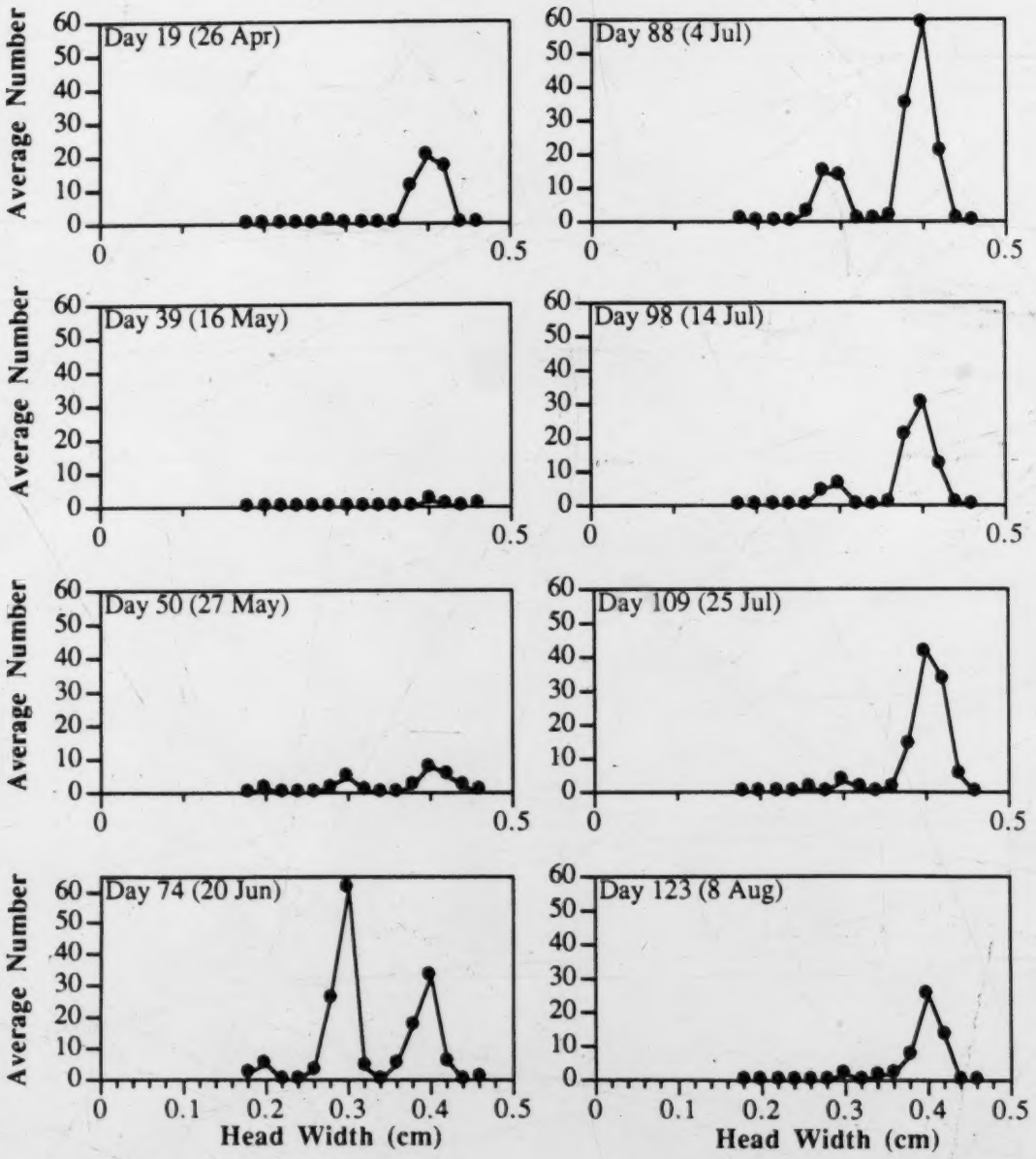


Figure 18. Head capsule widths plotted against average number of *Pericoma kincaidi* larvae in the Bigoray River, 1988.

DISCUSSION

There have been many studies on the ecology of macroinvertebrates on submerged wood. Workers have described invertebrate communities and quantified energy budgets of beaver ponds in streams. However, no published study has addressed the question of what aquatic invertebrates, if any, are found on the sticks and other substrates of beaver dams.

I asked several questions about aquatic invertebrates found on and in beaver dams of a brown-water stream of central Alberta.

1. Do differences exist between invertebrate populations on beaver dams and invertebrate populations in beaver pools of the Bigoray River in terms of population diversity? How are invertebrate communities on dams structured in terms of trophic relationships and habitat preferences?

2. How might disturbance affect the fauna of beaver dams?

3. What are the basic life cycle patterns of some of the invertebrates found on beaver dams?

Diversity.

To compare the diversity of invertebrate populations collected from beaver dams with the diversity of those collected from pools in the Bigoray River, I examined data collected in 1986 by H.F. Clifford. Diversity of invertebrates on beaver dams was consistently higher than that of invertebrates in beaver pools. Dam diversity was as much as twice as high as pool diversity on the same sampling date, and these differences were particularly marked in spring (May) and late summer (August).

Despite the non-quantitative sampling methods used to sample the two dams, and hence the rather variable sample sizes collected on each sampling date, faunal diversities on the two dams tended to be similar. Again, diversity peaked in May and in autumn. Peak diversities from the 1986 and 1989 samples were about 0.25, but summer values in 1989

were much lower than in 1986. Possibly this was due to the generally much smaller sample sizes of 1986. To calculate diversity, it is important to collect as many taxa as possible for a given sampling effort. Frost *et al.* (1971) observed that smaller samples (in terms of area) tended to be less consistent with each other and that only a relatively small proportion of the available individuals were captured. Mackey *et al.* (1984) examined the effects of reducing taxonomic level on taxon accumulation curves. At the family taxonomic level, one sample (a kick sample from a stream bed taken over about 5 minutes) was sufficient to collect over 90% of the families necessary for a representative list of taxa. They estimated that six samples provided a valid taxon list. At the genus level, no more than two samples were required to obtain 90% of the genera collected in six samples. Therefore, although the authors suggested that six samples were necessary to compile a representative list of taxa, two samples appeared to be adequate for the purposes of my study.

In short, the aquatic macroinvertebrate communities on beaver dams in the Bigoray River were more diverse than those found in the pools of the river immediately upstream of the dams. Diversity on the dams peaked in May and in autumn, at values of about 0.25.

Invertebrate community structure.

Beaver dams consist mainly of submerged and partially submerged wood, usually freshly cut (within 1 or 2 years) by beavers. Often, a large amount of allochthonous detritus is trapped behind and throughout the dam, and thus habitats available for invertebrates are diverse. Aquatic invertebrates may have an obligate association with wood or an opportunistic association. Obligates may require wood for feeding, as habitat for boring, or for case building (e.g. Trichoptera). Also obligates tend to be found mainly on wood instead of other substrates. Opportunists, as their name implies, use alternative habitats, and use wood for resting, as a refuge, for net attachment, as a substrate for

pupation and emergence, and for grazing the aufwuchs layer (Dudley and Anderson 1982).

The state of decay of wood is an important determinant of the invertebrate community found on it. New wood is mainly used as habitat. As the wood acquires an aufwuchs layer, collectors and grazers move in, but it is not until fungi invade the wood that it becomes soft enough to allow scrapers, gougers and shredders to ingest and abrade it. As fungi continue to penetrate the wood, borers may colonise the matrix. Finally detritivores such as oligochaetes help to complete the process of decay. If wood entering a stream is preconditioned on land, this allows speedier decay. Also, physical conditions in the stream affect decay rates. Wood debris is commonest in headwater streams where low streamflow causes less abrasion and displacement of the material and thus allows more extensive conditioning by decomposers. But in larger streams and during high water, where physical abrasion removes soft tissue and washes wood onto shore, the decay process slows. These processes normally take many years to complete (Dudley and Anderson 1982).

Most taxa found on beaver dams were collectors-gatherers, scrapers, or predators (engulfers, not piercers). But invertebrates that filter-feed, scavengers, shredders, and invertebrates that pierce plant or animal tissues were also represented (Table 5). Six of the most numerous taxa on the dams were filter-feeders, mainly simuliids and hydropsychids (48%, and 0.9% of the 1989 invertebrate total respectively). Larvae of these 2 taxa presumably use the wood as a solid substrate to anchor themselves or their nets for feeding. Smooth, relatively fresh wood tends to be suitable for such attachments. Beaver dams, particularly when being continually built up and modified by beavers, as was the case at my study sites, consist mostly of newly cut wood. This wood has generally not been preconditioned on land and therefore is little decayed before entering the water. Also, spates, such as the floods that occurred during 1989, are common, and often remove large portions of the dams. Therefore, wood turnover in beaver dams is probably higher than for wood trapped in quieter reaches of rivers. Dudley and Anderson (1982) found a "remarkably low" density and diversity of invertebrates on beaver dams in forested regions

of the western United States, and attributed this to the lengthy period required for microbial colonisation of fresh wood.

Dudley and Anderson (1982) found that less than 10% of invertebrates that they classified as closely associated with wood occurred on firm wood, and about 30% on firm wood that they had textured with grooves; whereas 20% of more opportunistically associated taxa were found on firm wood and 70% on grooved wood. Thus, it is likely that most taxa found in the Bigoray River are opportunistically associated with the wood of the beaver dams.

Considering collectors-gatherers, scrapers, scavengers, and shredders to have many detritivorous members, then of 72 taxa on dams found in the Bigoray River, more than half are detritivores. Of these, 15 were collectors-gatherers and 9 scrapers; these are characteristically found on wood that is in an early stage of decay. The remainder, 6 scavengers and 9 shredders, are found either on fungal invaded (and thus soft and relatively decayed) wood or, more probably in the detritus trapped in the dam. Pereira *et al.* (1982) examined the gut contents of over 100 insect taxa found on wood to determine their primary diet. Larvae and adults of 45 taxa had significant amounts of wood in their guts, and all xylophages were also detritivores but not all detritivores used wood. Thus, detritivores on beaver dams may feed on wood as well as detritus, but most likely only small twigs are sufficiently decayed to allow scrapers and shredders to use them, as most of the larger logs on the dams are relatively fresh.

A diverse array of predators also inhabited the dam, probably mainly opportunistic taxa that used wood for concealment, resting or protection, as well as for capturing prey.

Thus the invertebrate community found on beaver dams in the Bigoray River is characterised by a habitat consisting of new wood that has undergone little decay. Detritivores are common on the dams, but my samples did not differentiate between animals collected from decayed wood on the dams and trapped detritus. However, the absence of

detritivores (e.g. annelids) found only in very soft wood and borers (e.g. certain beetle larvae and tipulids) suggests that the wood in dams is not in an advanced state of decay. Although (in terms of requiring a wood habitat) most of the inhabitants of the dams are opportunists, many of the taxa are not found elsewhere in the Bigoray River. Obviously they require certain conditions found only on the dams, and in a sense may be viewed as obligates on beaver dams, at least in environments with limited habitat choices such as a silty, slow river system such as the Bigoray River.

As well as food and substrate availability on dams, physical conditions, such as water velocity, oxygen levels, and temperature differ between the dams and the rest of the river; and these factors will influence the distribution of invertebrate taxa found on the dams. Invertebrates from lotic erosional habitats were common in dam samples, but invertebrates normally found in lotic depositional and lentic littoral zones were also found in the samples (Table 6). This suggests that the beaver dams consist of more than one habitat for aquatic invertebrates.

Filter-feeding animals, some scrapers and collectors (especially mayflies, stoneflies some beetles and caddisflies) and a few predators are typically found in lotic-erosional habitats. Similar conditions are found where water flows freely over and around the wood in the dams. A lotic-depositional environment is created by jams of detritus behind and through dams. Here, detritivores and scavengers are found, these animals often burrowing in the detritus.

Finally, the beaver pond behind the dams provide a lentic habitat with both littoral and erosional regions suitable certain for certain chironomids, pelecypods, burrowing mayflies, leeches and oligochaetes. Faunal composition on beaver dams differed considerably from the invertebrates found in beaver pools in the Bigoray River. As frequently reported (e.g. Krebs 1985), both the pool and dam habitats supported communities of a few very common taxa and many comparatively rare taxa.

In samples of invertebrates from the beaver dams, I considered "common" taxa to be those making up more than 30% of the total number of invertebrates collected during the 1989 sampling season. This group (the simuliids and chironomids) was clearly separated from the remaining taxa and was designated group 1. Several of the remaining taxa, although mainly uncommon, made up a large proportion of a limited number of samples during the year. These taxa were placed in group 2, and each made up roughly 0.1% or more of the total fauna, or, excluding group 1, more than about 1.5% of the total fauna on dams #1 and #2. The remaining 34 (dam #1) to 48 (dam #2) rare taxa represented less than approximately 1.5% of the total fauna (excluding group 1) on the dams. These divisions of common, less common, and rare taxa were placed in groups 1, 2 and 3 respectively to facilitate comparisons (Tables 1 and 2).

The most common animals, i.e. those belonging to groups 1 and 2, belong to several different trophic groups; thus no one method of feeding is dominant (Tables 1,2 and 5). In terms of habitat, most of the more numerous animals preferred a fast-flowing (lotic-erosional) environment, although some of these could also tolerate slower water.

Several terrestrial animals were collected on dams (Tables 1 and 2) This indicates that beaver dams provide an interface between terrestrial and aquatic habitats. Dudley and Anderson (1982) found species richness to be greater on wood that extended from a river bank into the water than on completely submerged wood, and this may partially explain the high diversity of invertebrates found on beaver dams in the Bigoray River.

Beaver dams and disturbance.

Most dams are actively built and manipulated by beavers during the ice-free season. Also portions of the dams I studied were regularly disrupted by sampling. Thus dams can be considered disturbed environments. Clifford (1982) disrupted the substrate of the Bigoray River twice a month for 2.5 months and concluded that routine sampling in the Bigoray River, and in most streams, would have an undetectable effect on the structure of

the stream community. Many workers agree that stream invertebrates recolonise mainly by drift. I hypothesise that this disturbance effect (due to beavers or sampling) excludes few taxa from dams, because many aquatic macroinvertebrates can easily move from undisturbed regions to recolonise disturbed areas. Indeed, although records of exact sampling points on the dams under investigation were not kept, often one sample was taken from almost the same site as on the previous sampling date, and no differences between samples from the same dam on the same date were detected. This supports my hypothesis that, although dams were regularly disturbed in patches, the invertebrates recolonised disturbed areas rapidly. However, although taxa were probably not eliminated by the disturbance, some reduction in numbers of more sensitive taxa on the dam could have occurred. This could be due to the higher drift rate of animals from the dam or to their inability to recolonise as fast as their competitors.

Life Histories of *Pericoma kincaidi* (Diptera: Psychodidae) and Mermithidae (Nematoda) from Beaver Dams on the Bigoray River.

Life History of Pericoma kincaidi. Pericoma kincaidi (Diptera: Psychodidae, Psychodinae) was found sporadically in large numbers in the dams. Of 91 Psychodidae species recorded from America north of Mexico, 77 are Psychodinae. The presence of 76 species of this subfamily in the United Kingdom alone suggests that many species are yet to be described in the Nearctic region. In short, the Nearctic fauna is inadequately known (Quate and Vockeroth 1981). The larvae of *Pericoma* are described by Merritt and Cummins (1978) as burrowing in littoral regions of lentic habitats (e.g. in detritus) or depositional areas of lotic habitats. They obtain food as collectors or gatherers. The *P. bipunctata* complex (of which *P. kincaidi* is a member) is found from southern California to Alaska. *Pericoma kincaidi* is found in Washington, British Columbia, southern Alaska, and inland as far as Utah, Wyoming and Michigan, but has not been recorded in Alberta.

Thus, the Bigoray River records (subject to confirmation) extend the range of this species in a northeasterly direction into the Canadian prairies.

The *Pericoma kincaidi* population in the Bigoray River in 1988 appears to be univoltine, completing one generation per year. The species probably overwinters as fourth instar larvae, emerging in May and growing throughout the summer. It is possible that eggs also survive the winter, but there was no direct evidence of this. One pupa was found on the dams in 1989, but despite sampling nearby areas of the river, I was unable to find other pupae.

Future research could be designed to investigate several facets of this fly's life history. Once a successful laboratory breeding method is established, the effects of various factors such as temperature, on developmental rate, could be evaluated. Most of the ecological work on Psychodidae was carried out in the 1930's and 1940's on *Psychoda*, because several species of this genus are known to cause nuisances around trickling sewage filters and household drains (Headlee and Beckwith 1918, Fair 1934, Lloyd *et al.* 1940, Satchell 1947). The effects of water temperature on the life histories of *Psychoda* species have been examined in detail by several workers. At high water temperatures, *Psychoda* larvae are capable of rapid development. In fact, on the basis of this rapid development, Turner (1923) suggested *Psychoda alternata* would be a suitable subject for breeding and heredity studies. Between June and September, 1989, water temperatures in the Bigoray River were above 14°C. At these temperatures, at least two species of *Psychoda* could complete their life-cycle in less than 35 days (Lloyd 1937, Golightly 1940, Lloyd *et al.* 1940). Thus *Pericoma kincaidi* could possibly complete more than one life-cycle per year in the Bigoray River. Several steps could be taken to determine the number of generations completed by *P. kincaidi* per year. More frequent field sampling would probably find the first instar larvae, probably in May when larvae of the early instars first appear. Subsequent breeding of *Psychoda* in the laboratory at differing temperatures would establish the number of degree-days required for development. This could then be

compared with field data on temperature and life-cycle of *Pericoma*.

Larval *P. kincaidi* respire by means of spiracles at the posterior end of the abdomen. They hold these spiracles at the water surface for gas exchange. Thus, although able to stand short periods of submergence, they are susceptible to flooding; and populations therefore can be much reduced by freshets. For example, in 1989, only 66 psychodid larvae were taken from dams #1 and #2 between February and November; this was probably due to two summer floods, which would not only drown larvae, but would wash them off the dams. An interesting project could be collecting drift samples from the river above and below the dams to determine if *Pericoma* drifts, and, if so, what proportion is from the river channel and what proportion is from the dam. Also, is the drift of *Pericoma* affected by water level, current speed, and temperature?

Life History of Mermithidae. Much of the recent work on Mermithidae (Nematoda) has centred on the nematode's relationship with its blackfly host. The worm penetrates an early instar blackfly larva, develops, and emerges during the simuliid's last larval instar or the adult stage. The emergence of the nematode kills its host (Bailey *et al.* 1977, Colbo and Porter 1980). Mermithids vary in their host specificity, some being host specific, and others infecting all species they were exposed to in laboratory experiments (Colbo and Porter 1980). The rate of infection and number of mermithid larvae per host varies between the time of hatching of the host and development of the last instar of the host. When the parasite emerges from larval simuliids, the heaviest infections occur towards the downstream area of the simuliids' local distribution. Where they emerge from adult flies, the parasite tends to have a high infection rate at the upstream area of the simuliids' local distribution. This is due to the upstream migration of infected adult simuliids. Colbo and Porter (1980) found that the highest percentage of larvae infected in Newfoundland sites occurred between September and January; they suggested that simuliids and the free-living

larval mermiths commenced hatching at the same time, with the ratio of mermiths to simuliid larvae being initially high but dropping as the peak simuliid hatch occurs. I found that the free-living stages of the mermiths were most abundant in early June and were absent from samples by September. Larval Simuliidae were parasitised throughout the sampling season but mermithids reached their highest level relative to simuliid abundance in the summer (May to September).

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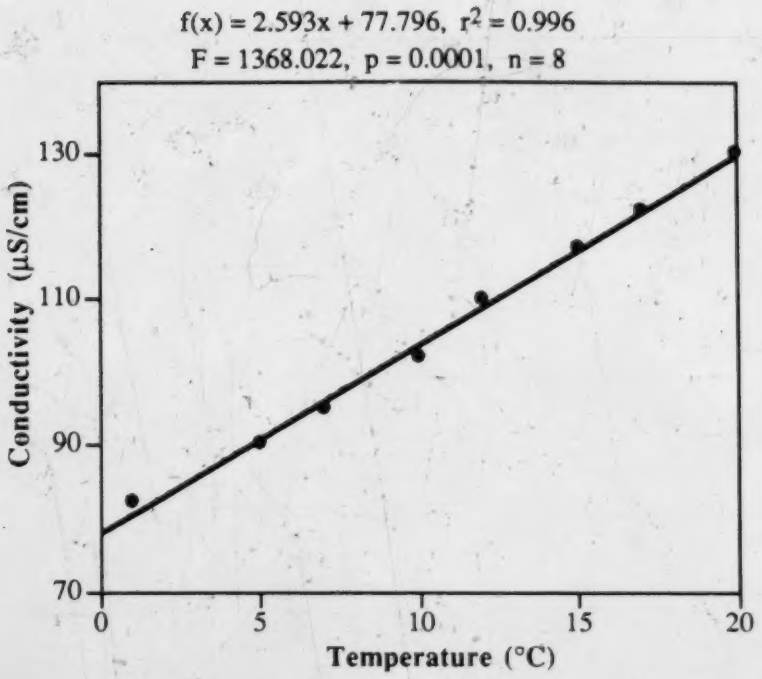
APPENDICES



Appendix 1: Standardisation curve of water conductivity against temperature.

Conductivity of a solution was measured in the laboratory at temperatures ranging from 1 to 20°C. Conductivity was significantly related to temperature (Appendix 1: $r^2 = 0.996$, $p < 0.005$, $n = 8$). The equation expressing the relationship between conductivity and temperature ($f(x) = 2.593x + 77.796$) was used to standardise the conductivity values obtained for the Bigoray River at different temperatures, to those that would be expected at 15°C.

Appendix 2. Trophic relationships and habitat of aquatic invertebrates found on beaver dams in the Bigoray River. All taxa are immature except those indicated as P = pupae or A = adult. (Sources: Merritt and Cummins 1978, Pennak 1978, Borrer *et al.* 1981.)

General classification system for aquatic insect trophic relations (Merritt and Cummins 1978):

—Collectors are detritivores that either filter fine particulate organic matter (FPOM) from the water, or gather or deposit feed (on sediment or on the surface film).

—Piercers are either herbivores that pierce cells and tissues of living vascular hydrophytes and filamentous algae and suck fluids from them, or carnivores that pierce the cells and tissues of their prey.

—Scrapers feed on periphyton (attached algae and other material) by grazing hard surfaces

—Shredders are either herbivores feeding on living vascular hydrophyte plant tissue, or detritivores that chew or bore into decomposing vascular plant tissue or wood — coarse particulate organic matter (CPOM).

—Engulfers are carnivores, and consume whole animals or parts of them.

	Trophic Relationships	**Habitat**
Diptera		
Chironomidae	Generally (a) collectors-gatherers and filterers, or (b) engulfers (predators) and piercers-predators	All types
Simuliidae	Generally collectors-filterers	Generally lotic-erosional
Tipulidae	Generally shredders-detritivores, collectors-gatherers	Generally lentic-littoral, lotic-erosional and depositional (detritus)
Ceratopogonidae	Generally engulfers-predators, collectors-gatherers	Generally lentic-littoral (including tree-holes and temporary pools), lotic-depositional (margins and detritus)
Pericoma (Psychodidae)	Collectors-gatherers	Lotic-depositional (margins), lentic-littoral (detritus)
Pericoma (P)	———	
Ephemeroptera		
Baetis (Baetidae)	Collectors-gatherers (detritus, diatoms), scrapers	Lotic-erosional and depositional, lentic-littoral
Caenis (Caenidae)	Collectors-gatherers (scrapers)	Lotic-depositional, lentic-littoral (sediments)
Paraleptophlebia (Leptophlebiidae)	Collectors-gatherers (detritus, diatoms), shredders-detritivores	Lotic-erosional (sediments and detritus)

Appendix 2, continued

	Trophic Relationships	Habitat
Stenacron (Heptageniidae)	Collectors-gatherers, scrapers	Lotic and lentic-erosional
Stenonema (Heptageniidae)	Collectors-gatherers, scrapers	Lotic and lentic-erosional
Ephemera (Ephemeridae)	Collectors-gatherers, (engulfers)	Lotic and lentic - depositional
Small Ephemeroptera	———	
Plecoptera		
Amphinemura (Nemouridae)	Shredders-detritivores, collectors-gatherers	Lotic erosional and depositional (detritus)
Isoperla (Perlodidae)	Engulfers (predators on Chironomidae, Ephemeroptera and Plecoptera), collectors-gatherers	Lotic—erosional and depositional
Small Plecoptera	———	
Unidentified Ephemeroptera/Plecoptera	———	
Trichoptera		
Hydropsyche (Hydropsychidae)	Collectors-filterers (algae, detritus, animals)	Lotic-erosional, some lentic-erosional
Cheumatopsyche (Hydropsychidae)	Collectors-filterers (algae, detritus, some animals)	Lotic-erosional (especially warmer streams and rivers)
Small Hydropsychidae	———	
Hydroptila (Hydroptilidae)	Piercers-herbivores, scrapers	Lotic-erosional and depositional (including seeps)
Rhyacophila (Rhyacophilidae)	Engulfers (predators), a few scrapers, collectors-gatherers, shredders-herbivores (chewers)	Lotic-erosional
Lepidostoma (Lepidostomatidae)	Shredders-detritivores (chewers)	Lotic-erosional and depositional (detritus) (headwater streams and springs)
Limnephilidae	Generally shredders-detritivores (chewers), collectors-gatherers, scrapers	All types of lentic and lotic habitats
Brachycentrus (Brachycentridae)	Collectors-filterers (algae, animals), scrapers	Lotic-erosional (on logs, branches or vascular hydrophytes)

Appendix 2, continued

	Trophic Relationships	Habitat
Oecetis (Leptoceridae)	Engulfers (predators), shredders-herbivores (chewers)?	Lotic-erosional and depositional, lentic littoral
Trichoptera	———	
Coleoptera		
Agabus (Dytiscidae)	Piercers-predators	Lotic-erosional and depositional, lentic-vascular hydrophytes
Agabus (A) (Dytiscidae)	As for larvae	As for larvae
Amphizoa (Amphizoidae)	Engulfers (predators-especially on Plecoptera)	Lotic-erosional (especially logs)
Brychius (Haliplidae)	Scrapers, piercers-herbivores	Lotic (and lentic) erosional
Brychius (A) (Haliplidae)	As for larvae	As for larvae
Carabidae (A)	———	
Dytiscidae	Piercers-carnivores	Lotic-depositional
Endalus (A) (Curculionidae)	Shredders-herbivores (chewers and miners)	Lentic-vascular hydrophytes (emergent zone)
Gyrinidae (A)	Generally engulfers (predators) and surface film (neuston) scavengers	Lentic and lotic-depositional
Gyrinus (Gyrinidae)	Engulfers (predators) and neuston scavengers	Lentic and lotic-vascular hydrophytes
Haliplus (A) (Haliplidae)	Piercers and shredders-herbivores	Lentic-vascular hydrophytes
Laccornis (A) (Dytiscidae) Laccornis only reported in East (Merritt and Cummins 1978)	Piercers-carnivores	Lentic-vascular hydrophytes
Elmidae	Generally collectors-gatherers, scrapers	Lotic-erosional (cobbles and gravel)
Staphylinidae	Engulfers (predators)	Generally beaches, stream shores, in leaf litter
Coleoptera	———	
Coleoptera (A)	———	

Appendix 2, continued

	Trophic Relationships	Habitat
Hemiptera		
Corixidae	Generally piercers-herbivores and some carnivores, some engulfers (predators)	Generally lentic-vascular hydrophytes, lotic-depositional (vascular hydrophytes)
Homoptera	———	
Odonata		
Somatochlora (Corduliidae)	Engulfers (predators)	Lentic-littoral (bogs), lotic-depositional (springs)
Leucorrhinia (Libellulidae)	Engulfers (predators)	Lentic-vascular hydrophytes (including bogs)
Aeshna (Aeshnidae)	Engulfers (predators)	Lotic-erosional and depositional (sand), lentic-littoral (sand)
Odonata	———	
Thysanoptera	———	
Araneidae	———	
Hydracarina	Generally piercers-carnivores (and parasites)	Lentic-littoral (vascular hydrophytes), and lotic-vascular hydrophytes
Gammaridae		
Hyalella azteca	Scavengers (aufwuchs, detritus)	Lentic and lotic-often associated with aquatic vegetation
Mollusca		
Pelecypoda		Rivers on stable substrate (sand, gravel and detritus), some lentic
Pisidium (Sphaeriidae)	Collectors- filterers	Lake bottoms and lotic-burrowers

Appendix 2, continued

	Trophic Relationships	Habitat
Physa (Physidae)	Omnivores	Moderate amount aquatic vegetation and organic debris
Limnaeidae		
Armiger crista (Planorbidae)		
Planorbidae		
Mollusca	———	
Hirudinea	Carnivores, scavengers and blood-suckers	Lentic and slow lotic
Oligochaeta	Generally detritivores	Lentic and lotic-mud, debris, and in filamentous algae
Nematomorpha	Do not feed	Lentic and lotic-shallow water
Nematoda		
Free-living nematodes	Detritivores, herbivores, and carnivores	All types of freshwater habitats
Mermithidae in Simuliidae	———	
Free-living Mermithidae	———	
Parasite in chironomids	———	
Tardigrada	Piercers-herbivores	On aquatic mosses, algae, vascular hydrophytes, or lentic mud and debris